QK
S20
.A512
BOT

AMERICAN
FERN JOURNAL

QUARTERLY JOURNAL OF THE AMERICAN FERN SOCIETY

VOLUME 111 NUMBER 4 October-December 2021

THE AMERICAN FERN SOCIETY

Council for 2020

EMILY SESSA, Department of Biology, University of Florida, Gainesville, FL 32611 — *President*

JOSHUA DER, Department of Biological Science, California State University, Fullerton, Fullerton, CA 92831 — *President Elect*

JORDAN METZGAR, Massey Herbarium, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061 — *Secretary*

ERIC SCHUETTPELZ, Smithsonian NMNH Botany (MRC 166), PO Box 37012, Washington DC 20013-7012 — *Treasurer*

SALLY CHAMBERS,Botany Department, Marie Selby Botanical Gardens, 1534 Mound St., Sarasota FL 34236 — *Membership Secretary*

WESTON TESTO, Department of Biological and Environmental Sciences, University of Gothenburg, Sweden — *Webmaster*

CHRISTOPHER H. HAUFLER, Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045 — *Journal Editor*

DARLA HARRIS, 16240 Hartman Rd., Magnolia, TX 77355

NIKISHA PATEL, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269 — *Bulletin Editors*

AMERICAN FERN JOURNAL

EDITOR

CHRISTOPHER H. HAUFLER ... Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, e-mail: vulgare@ku.edu

MANAGING EDITOR

TOM A. RANKER..... School of Life Sciences, University of Hawai'i at Mānoa, Honolulu, HI 96822

ASSOCIATE EDITORS

SUSAN FAWCETT ..... University and Jepson Herbaria, University of California, Berkeley, CA 94720

GARY K. GREER ..... Biology Department, Grand Valley State University, Allendale, MI 49401

JUDITH A. JERNSTEDT ..... Department of Plant Sciences, University of California, Davis, CA 95616

FAY-WEI LI ..... Boyce Thompson Institute, Cornell University, Ithaca, NY 14853

SCOTT A. M. MCADAM ..... Botany and Plant Pathology, Purdue University, West Lafayette, IN 47907

KLAUS MEHLTRETER.....Instituto de Ecología, A.C., Xalapa 91070, Veracruz, Mexico

ROBBIN C. MORAN..... New York Botanical Garden, Bronx, NY 10458

JEFFERSON PRADO ... UNESP, IBILCE, Depto. de Zoologia e Botânica, São José do Rio Preto, SP, Brasil

CARL J. ROTHFELS ... Department of Integrative Biology, University of California, Berkeley, CA 94720

ALEJANDRA VASCO ..... Botanical Research Institute of Texas, Fort Worth, TX 76107

American Fern Journal 111(4):223–250 (2021)
Published on 5 November 2021

Looking Back on 130 Years of Fern and Lycophyte Research in Glacier National Park, Montana: A Modern Taxonomic Account

SMITHSONIAN
OCT 27 2022
LIBRARIES

KEEGAN HERON[1]
Department of Biology, Duke University, Durham, NC 27708, USA
heron.keegan@gmail.com

MICHAEL D. WINDHAM[1]*
Department of Biology, Duke University, Durham, NC 27708, USA
michael.windham@duke.edu

DONALD R. FARRAR
Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011, USA
dfarrar@iastate.edu

KATHLEEN M. PRYER
Department of Biology, Duke University, Durham, NC 27708, USA
pryer@duke.edu

ABSTRACT.—Glacier National Park encompasses over one million acres in the mountains of northwestern Montana, along the United States–Canada border. Our survey of online databases indicates that the earliest extant fern and lycophyte collections from this area were taken by Robert S. Williams in 1892. In the summer of 1919, Paul C. Standley, a botanist with the United States National Museum, conducted a survey of the flora of the newly created Park and recorded 39 species of ferns and lycophytes. In 2002, a revised flora for the Park by Peter Lesica increased this number to 61. Here we summarize 130 years of collections-based research on the ferns and lycophytes of Glacier National Park, documenting how our understanding of the flora has changed through time. In the summer of 2019, the lead author conducted a field survey to relocate as many ferns and lycophytes as possible within park boundaries. In parallel, we scoured herbarium online portals and databases for high-resolution digitized specimen images to confirm or refute historical vouchers of ferns and lycophytes collected from the Park. In a few cases, specimen loans were requested from herbaria to confirm our determinations. The results from our combined field and online herbarium studies are presented here. Of the 61 taxa recognized by Lesica in 2002, we were able to confirm all but seven. In sum, we recognize here a total of 71 fern and lycophyte taxa for the Park. Most previously unreported taxa belong to *Botrychium,* a genus that has seen a flurry of recent taxonomic work by co-author Farrar and collaborators. These new data are presented here together with updated nomenclature and discussion to provide a current taxonomic account of the fourteen fern and lycophyte families known to occur in Glacier National Park. We anticipate this study will provide a useful foundation for further investigations in the Park.

KEY WORDS.—ferns, herbarium online portal databases, lycophytes, Paul C. Standley, Peter Lesica

---

[1] Equal contributions

*Author for correspondence: michael.windham@duke.edu

This research is dedicated to the following indigenous American peoples: Blackfeet (Niitsitapi or Siksikaitsitapi), Kootenai (Ktunaxa or Ksanka), Pend d'Oreille (Qlispé or Kalispel), and Salish (Séliš), caretakers of this land before it was designated Glacier National Park in 1910.

Located in northwestern Montana, Glacier National Park (often referred to herein simply as the "Park") comprises over one million acres of towering mountains, heavily forested valleys, alpine meadows, raging meltwater streams, and the iconic glaciers (or what is left of them) that are its namesake (Hall and Fagre, 2003; Lesica, 2002; Fig. 1A). The Park straddles the Continental Divide, sharing a border with Canada to the north, as well as with the Blackfeet Nation (one of the largest indigenous American communities) to the east, and the Flathead National Forest to the west. In 1932, Waterton Lakes National Park in Alberta, Canada was combined with Glacier National Park to form the world's first International Peace Park, a United Nations Education, Scientific and Cultural Organization (UNESCO) World Heritage site (Thomas and Mow, 2016).

In the summer of 1919, nine years after Glacier National Park was established, Paul C. Standley, a botanist employed by the United States National Museum (Smithsonian Institution), conducted a survey of the flora of the newly created Park. Among the over 900 specimens he collected that year, Standley (1920, 1921) catalogued 39 species of ferns and lycophytes, two more than had been previously recorded for the entire state of Montana (Fitzpatrick, 1904). In 2002, when Peter Lesica published his comprehensive *Flora of Glacier National Park, Montana* the number of ferns and lycophytes reported for the Park had risen to 61.

In the summer of 2019, a century after Standley's survey of the Park's flora, and while employed as a botanical technician by Glacier National Park, the lead author set out to relocate as many of the reported ferns and lycophytes as possible. In parallel, the authors also scoured recent publications and several regional herbarium online portals (*e.g.*, The Consortium of Pacific Northwest Herbaria [https://www.pnwherbaria.org/]) for new Park records, to confirm or refute (to the best of our ability) the identification of historical records of digitized ferns and lycophytes collected in the Park. Here, we present the results of our combined field and online herbarium studies, together with revised nomenclature, to provide an update on the fern and lycophyte flora of Glacier National Park. We anticipate that this study will be a useful foundation for future systematic and ecological investigations in the Park.

Materials and Methods

Study Area.—Glacier National Park is located in the northwestern corner of Montana along the spine of the Rocky Mountains (Fig. 1A, B). It encompasses over 1 million acres (4,000 km^2), over 130 named lakes, more than 1,000 different species of vascular plants (Lesica, 2002), hundreds of species of animals, and six mountain tops exceeding 3000 m. It is estimated that there

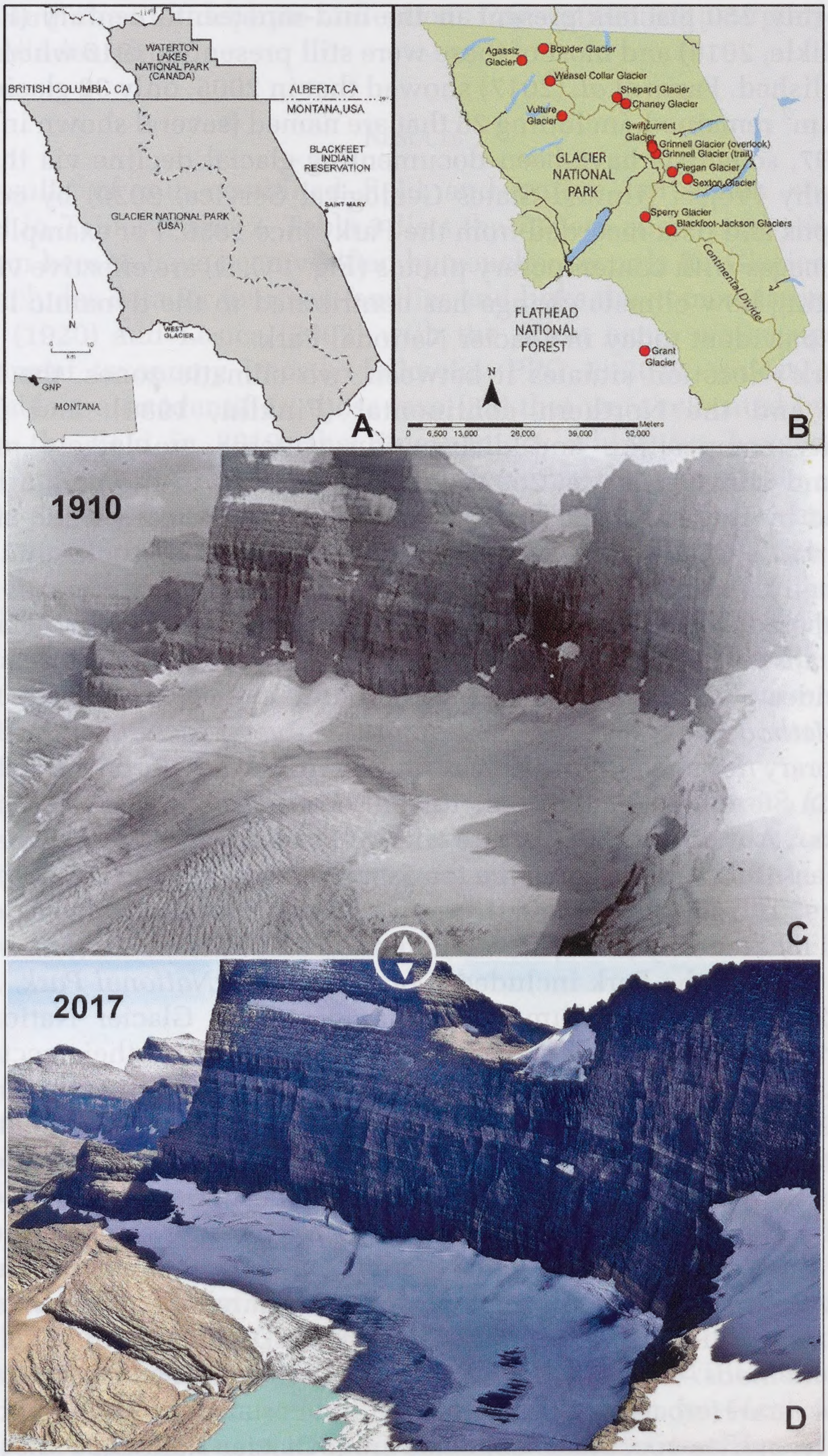

FIG. 1. Glacier National Park, Montana. A. Map of Glacier National Park and surrounding areas, modified from Resler and Tomback (2008); B. Red dots represent glaciers throughout the Park that have been re-photographed by USGS since 1997; C. Grinnell Glacier, 1910, photo by Morton Elrod, K. Ross Toole Archives, University of Montana; D. Grinnell Glacier, 2012, photo by Dan Fagre, USGS. Map in B, and photos in C and D from the USGS Repeat Photography Project http://nmrsc.usgs.gov/repeatphoto.

were roughly 150 glaciers present in the mid-nineteenth century (Fagre and Martin-Mikle, 2018) and most of these were still present in 1910 when the Park was established. Fagre *et al.* (2017) showed that in 2005, only 32 glaciers larger than 0.1 km^2 remained, including 26 that are named (several shown in Fig. 1B). Since 1997, scientists have been documenting glacial decline via the Repeat Photography Project (United States Geological Service, 2020) by comparing photographs and data recorded from the Park since 1850. For example, pairing historic images with contemporary photos (Fig. 1 C, D) are effective visuals for documenting how climate change has contributed to the dynamic landscape changes so evident today in Glacier National Park.

The Park's location situates it between two climatic zones, the Northern maritime and the Northern continental (Finklin, 1986), and its plant community composition and distribution patterns are largely related to geology and climate (Lesica, 2002). Weather patterns in the park are heavily influenced by Pacific storms coming from the west and cold arctic air arising from the north. These wind currents, known locally as chinook winds, can be exceptionally strong on the east side of the park, as air makes its way unencumbered from the crest of the mountains to the Great Plains. These wind patterns cause a pronounced difference in the vegetative communities between the two sides of the Park (Lesica, 2002).

Field Methods.—In 2019, in an attempt to survey Glacier National Park for contemporary fern records, the lead author followed the same approaches outlined in Standley (1920) by "visiting all portions of the Park normally seen by tourists." Although infrastructure within the Park has changed considerably over the last 100 years, many of the tourist attractions more easily accessible in the early 20th century remain the same today. All locations specifically described by Standley (1920) were visited. Additional sources that were used to locate ferns in the Park included *Flora of Glacier National Park, Montana* (Lesica, 2002), the herbarium collection located at Glacier National Park headquarters, and the Park staff who generously shared their accumulated knowledge of fern locations. Ferns and lycophytes were actively searched for anywhere from 25 to 35 hours per week from May 15 to August 15 in the summer of 2019. A significant part of this was spent travelling to various parts of the Park, both by car and by foot, and locations where species had historically been found were prioritized. Upon locating a target species, its GPS coordinates, aspect, and habitat were noted, and photographs were taken (where available, photographs were posted to iNaturalist (2021) and are listed in Table 1 according to their unique iNaturalist ID number).

Online methods.—Our research utilized available online resources to search through several Herbarium Consortium Online Portals for recent and historical fern and lycophyte specimens collected from Glacier National Park that were available as high-resolution images and could be examined for identification accuracy (see Table 1). These included: The SEINet North American Plant Portal Network (https://swbiodiversity.org/); The Consortium of Pacific Northwest Herbaria (https://www.pnwherbaria.org/); The Smithsonian Department of Botany Collections (https://collections.nmnh.si.edu/search/

botany/); and The Pteridophyte Collections Consortium (https://pteridoportal.org/portal/index.php).

Results

The results of our combined field and online herbarium studies are presented in Tables 1 and 2. Table 1 lists the 71 fern and lycophyte taxa that we confirm here to have been verified by voucher records for Glacier National Park. It includes data for fourteen families and links the nomenclature used by Standley (1920) and Lesica (2002) with the taxon name we accept here to reflect current taxonomy (mostly following PPG 1, 2016, unless otherwise noted). Table 1 also identifies: those taxa (33) that were relocated by the lead author in the field in 2019; the timespan for which we have confirmed historical collections of each taxon based on metadata available in online herbarium databases; and a representative voucher specimen for each taxon.

Of our 71 confirmed taxa, the majority belong to the eusporangiate ferns (32 in Equisetaceae and Ophioglossaceae) and lycophytes (14 in Isoëtaceae, Lycopodiaceae, and Selaginellaceae). Leptosporangiate ferns are represented by 25 taxa, and only one of these (a hybrid) is newly reported here for the Park. The most species-rich genera in the Park are *Botrychium* and *Equisetum*, with 19 and 10 taxa, respectively. These are also the two genera that are most difficult for the non-specialist to find and/or identify accurately.

Table 2 lists the seven fern and lycophyte taxa included by Lesica (2002) that we were unable to verify for Glacier National Park, plus two other records that exist only as annotations on herbarium specimens. In a couple of cases, although we did see a few vouchers (not listed) purporting to represent a reported taxon, we determined them to be inconclusive and in need of further study.

Discussion

The number of fern and lycophyte taxa confirmed for Glacier National Park has increased from 0 to 71 in the last 130 years, with slightly more than half of these collected by Standley (1920). Field studies over the last century have added about 30 more taxa. These more recent discoveries have been driven by a variety of factors. Foremost among these is improved access to the wilderness that still comprises 95% of the Park. A combination of >100 miles of roads and >700 miles of maintained trails now provide a gateway to much more of the Park than was accessible to early collectors like R. S. Williams and P. C. Standley. The prodigious accumulation of knowledge on local ferns and lycophytes documented here also represents the cumulative efforts of scores of botanists, with many of their collections now becoming widely accessible through online portals. In the past decade, the digitization of herbaria has become a global enterprise with millions of high-resolution specimen images and their associated metadata now being easily accessible in online public databases (Page *et al.*, 2015; Soltis, 2017). Our access to these images (see

TABLE 1. Lycophyte and fern taxa **confirmed** for Glacier National Park in this study. Classes, subclasses, and families are organized phylogenetically following the classification in PPG 1 (2016). For information on the rarity status of any of these taxa, consult NatureServe (2021).

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
Lycopodiopsida (lycophytes)						
Lycopodiaceae	*Dendrolycopodium dendroideum* (Michx.) A. Haines	*Lycopodium obscurum*	*Lycopodium dendroideum*	1892-1999	ID89723481	Standley 18859 (US)
	Diphasiastrum alpinum (L.) Holub	*Lycopodium alpinum*	*Diphasiastrum alpinum*	1919-2009	—	Standley 17957 (US)
	D. complanatum (L.) Holub	*Lycopodium complanatum*	*Diphasiastrum complanatum*	1892-2006	ID89716171	Standley 18575 (US)
	Huperzia continentalis Testo, A. Haines & A.V. Gilman	—	*Huperzia haleakalae*	1917-2019	—	Barkley 1735 (WTU)
	H. continentalis × *H. occidentalis*	*Lycopodium selago*	—	1895-1935	—	Maguire 453 (GH)
	H. occidentalis (Clute) Kartesz & Gandhi	—	*Huperzia occidentalis*	1932-1976	—	Maguire 454 (GH)
	H. selago (L.) Bernh. ex Shrank. & Mart.	—	—	1921-2013	—	Jack 2324 (GH)
	Lycopodium annotinum L.	*Lycopodium annotinum*	*Lycopodium annotinum*	1892-1994	ID89739094	Standley 16045 (US)
	L. lagopus (Laest. ex C. Hartm.) G. Zinserl. ex Kuzen.	*Lycopodium clavatum monostachyon*	*Lycopodium lagopus*	1919-1985	—	Standley 18523 (US)
Isoëtaceae	*Isoëtes bolanderi* Engelm.	—	*Isoëtes bolanderi*	1994	—	Damm & Christian s.n. (Glacier National Park Herbarium 23682[3])
Selaginellaceae	*Selaginella densa* Rydb. var. *densa*	*Selaginella densa p.p.*	—	1919	—	Standley 15318 (US)
	S. densa Rydb. var. *scopulorum* (Maxon) R.M. Tryon	*Selaginella densa p.p.*	*Selaginella scopulorum*	1901-1996	ID89738047	Standley 15732 (US, holotype)

TABLE 1. Continued.

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
	S. densa Rydb. var. *standleyi* (Maxon) R.M. Tryon	*Selaginella densa p.p.*	*Selaginella standleyi*	1917-1949	—	Standley 17228 (US, holotype)
	S. wallacei Hieron.	*Selaginella wallacei*	*Selaginella wallacei*	1917-1993	ID89738495	Standley 17164 (US)
Polypodiopsida (ferns) Equisetidae						
Equisetaceae	*Equisetum arvense* L.	*Equisetum arvense*	*Equisetum arvense*	1910-2011	√	Standley 16727 (US)
	E. fluviatile L.	*Equisetum fluviatile*	*Equisetum fluviatile*	1910-1971	√	Standley 16027 (US)
	E. hyemale L. subsp. *affine* (Engelm.) Calder & Roy L. Taylor	*Equisetum hyemale*	*Equisetum hyemale*	1901-1966	√	Standley 16519 (US)
	E. laevigatum A. Braun	*Equisetum kansanum*	*Equisetum laevigatum*	1903-1996	ID89995871	Standley 16623 (US)
	E. pratense Ehrh.	—	*Equisetum pratense*	1934-1980	—	Maguire & Piranian 5425 (UTC)
	E. scirpoides Michx.	—	*Equisetum scirpoides*	1978-1980	—	Benham 408 (SAT)
	E. sylvaticum L.	*Equisetum sylvaticum*	*Equisetum sylvaticum*	1910-1998	√	Standley 15246 (US)
	E. variegatum Schleich. ex F. Weber & D. Mohr subsp. *variegatum*	*Equisetum variegatum p.p.*	*Equisetum variegatum* subsp. *variegatum*	1910-1993	√	Standley 16743 (US)
	E. × *ferrissii* Clute *(hyemale* × *laevigatum)*	*Equisetum praealtum; E. variegatum p.p.*	—	1919-2012	—	Standley 17614 (US)
	E. × *trachyodon* A. Braun *(hyemale* × *variegatum)*	*Equisetum variegatum p.p.*	—	1919-1933	—	Standley 18660 (US)
Polypodiopsida (ferns) Ophioglossidae						
Ophioglossaceae	*Botrychium ascendens* W.H. Wagner	—	—	2005	—	Farrar AS050623 (ISC)
	B. campestre W.H. Wagner & Farrar var. *campestre*	—	—	2005	—	Farrar CACA050623 (ISC)

TABLE 1. Continued.

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
	B. campestre W.H. Wagner & Farrar var. *lineare* (W.H. Wagner) Farrar	—	—	2005	—	Farrar CALI050623 (ISC)
	B. "*campestre* × *tunux* (4x)"	—	—	2005	—	Farrar CAxTU050623 (ISC)
	B. crenulatum W.H. Wagner	—	—	2005	—	Farrar CR050623 (ISC)
	B. furculatum S.J. Popovich & Farrar (previously known informally as *B. adnatum* ined.)	—	—	1996-2005	—	Farrar FL050621 (ISC); Wagner FL980625 (ISC)
	B. gallicomontanum Farrar & Johnson-Groh	—	—	2005	—	Farrar GA050621 (ISC)
	B. hesperium (Maxon & R.T. Clausen) W.H. Wagner & Lellinger	—	*Botrychium hesperium*	1987-1999	—	Ahlensberger & Lesica 4422 (US)
	B. lanceolatum (S.G. Gmel.) Ångstr.	—	*Botrychium lanceolatum* subsp. *lanceolatum*	1976-1994	—	Wagner & Wagner 78511 (MICH)
	B. michiganense W.H. Wagner ex A.V. Gilman, Farrar & Zika	—	—	2005	—	Farrar MC050621 (ISC)
	B. minganense Vict.	—	*Botrychium minganense*	1919-2015	—	Wagner & Wagner 78523 (MICH)
	B. montanum W.H. Wagner	—	*Botrychium montanum*	1954-1978	—	Wagner & Wagner 78532 (MICH, paratype)
	B. paradoxum W.H. Wagner	—	*Botrychium paradoxum*	1978-1998	—	Wagner 78547 (MICH, paratype)

TABLE 1. Continued.

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
	B. pinnatum H. St. John	—	*Botrychium pinnatum*	1976-1996	—	Lesica 6377 (MONTU)
	B. simplex E. Hitchc. var. *simplex*	—	*Botrychium simplex*	2001	—	Farrar SISI050621 (ISC)
	B. spathulatum W.H. Wagner	—	—	2005	—	Farrar SP050623 (ISC)
	B. tunux Stensvold & Farrar	*Botrychium lunaria p.p.*	*Botrychium lunaria p.p.*	2005	—	Farrar TU050623 (ISC)
	B. × *watertonense* W.H. Wagner	—	—	1998	—	Wagner WA980625 (ISC)
	B. yaaxudakeit Stensvold & Farrar	*Botrychium lunaria p.p.*	*Botrychium lunaria p.p.*	2001-2005	—	Farrar YA050622 (ISC)
	Botrypus virginianus (L.) Michx.	*Botrychium virginianum europaeum*	*Botrychium virginianum*	1901-1994	ID89736207	Standley 16945 (US)
	Ophioglossum pusillum Raf.	—	*Ophioglossum pusillum*	1993	—	Lesica & Bacon 6264 (MONTU)
	Sceptridium multifidum (S.G. Gmel.) Nishida ex Tagawa	*Botrychium silaifolium*	*Botrychium multifidum*	1901-1993	ID89724241	Standley 18585 (US)
Polypodiopsida (ferns) Polypodiidae						
Aspleniaceae	*Asplenium viride* Huds.	*Asplenium viride*	*Asplenium trichomanes-ramosum*	1901-2000	ID89737114	Standley 15368 (US)
Athyriaceae	*Athyrium distentifolium* Tausch ex Opiz subsp. *americanum* (Butters) Hultén	*Athyrium americanum*	*Athyrium alpestre* var. *americanum*	1895-1976	ID89736903	Standley 16841 (US)

TABLE 1. Continued.

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
	A. filix-femina (L.) Roth subsp. *cyclosorum* (Rupr.) C. Chr.	*Athyrium filix-femina*	*Athyrium filix-femina* var. *cyclosorum*	1892-1969	ID89735691	Standley 15372 (US)
Cystopteridaceae	*Cystopteris fragilis* (L.) Bernh. subsp. *fragilis*	*Filix fragilis*	*Cystopteris fragilis*	1901-1976	ID89735958	Standley 16808 (US)
	C. montana (Lam.) Bernh. ex Desv.	—	*Cystopteris montana*	1932	—	Rugg s.n. (US; WTU)
	Gymnocarpium disjunctum (Rupr.) Ching	*Dryopteris linnaeana*	*Gymnocarpium disjunctum*	1901-1967	ID89737996	Standley 15650 (US)
	G. dryopteris (L.) Newm.	—	*Gymnocarpium dryopteris*	1921-1932	—	Maguire 424 (GH)
	G. × *brittonianum* (Sarvela) Pryer & Haufler *(dryopteris* × *disjunctum*)	—	—	1901-1935	—	Vreeland 969 (CAN; US)
Dennstaedtiaceae	*Pteridium aquilinum* (L.) Kuhn subsp. *pubescens* (Underw.) J.A. Thomson, Mickel & Mehlt.	*Pteridium aquilinum pubescens*	*Pteridium aquilinum*	1903-1960	ID91645636	Yuncker & Yuncker 7006 (DUKE)
Dryopteridaceae	*Dryopteris carthusiana* (Vill.) H.P. Fuchs	*Dryopteris dilatata p.p.*	*Dryopteris carthusiana*	1919-1999	ID89996468	Standley 18514 (US)
	D. cristata (L.) A. Gray	*Dryopteris cristata*	*Dryopteris cristata*	1901-2000	—	Standley 18527 (US)
	D. expansa (C. Presl) Fraser-Jenk. & Jermy	*Dryopteris dilatata p.p*	*Dryopteris expansa*	1901-1983	ID89717305	Standley 16488 (US)
	D. filix-mas (L.) Schott	*Dryopteris filix-mas*	*Dryopteris filix-mas*	1895-1996	ID89739486	Standley 15362 (US)
	Polystichum andersonii Hopkins	*Polystichum andersonii*	*Polystichum andersonii*	1919-1980	—	Standley 17443 (US)
	P. lonchitis (L.) Roth	*Polystichum lonchitis*	*Polystichum lonchitis*	1892-1983	ID89716066	Standley 15210 (US)

TABLE 1. Continued.

Classification	Taxon name adopted in this study	Taxon name in Standley (1920)	Taxon name in Lesica (2002)	[1]Time span of records	[2]Observed in 2019	Representative voucher specimen
	P. munitum (Kaulf.) C. Presl	—	*Polystichum munitum*	1994	ID89737788	Spribille s.n. (Glacier National Park Herbarium 21798)
Polypodiaceae	*Polypodium hesperium* Maxon	*Polypodium hesperium*	*Polypodium hesperium*	1900-1994	ID90499912	Standley 16685 (US)
Pteridaceae	*Adiantum aleuticum* (Rupr.) C.A. Paris	*Adiantum pedatum aleuticum*	*Adiantum aleuticum*	1892-1971	ID89737364	Standley 16817 (US)
	Aspidotis densa (Brack.) Lellinger	*Cheilanthes siliquosa*	*Aspidotis densa*	1895-1993	ID90501100	Standley 15576 (US)
	Cryptogramma acrostichoides R. Br.	*Cryptogramma acrostichoides*	*Cryptogramma acrostichoides*	1895-1978	ID89737581	Standley 17990 (US)
	C. stelleri (S.G. Gmel.) Prantl	*Cryptogramma stelleri*	*Cryptogramma stelleri*	1895-2009	ID89737009	Standley 17143 (US)
	Myriopteris gracillima (D.C. Eaton) Grusz & Windham	*Cheilanthes gracillima*	*Cheilanthes gracillima*	1895-1995	ID89736698	Standley 15558 (US)
Thelypteridaceae	*Phegopteris connectilis* (Michx.) Watt	—	*Phegopteris connectilis*	1909-1988	ID89737196	Jones s.n. (WIS)
Woodsiaceae	*Woodsia scopulina* D.C. Eaton subsp. *scopulina*	*Woodsia scopulina*	*Woodsia scopulina*	1901-1998	√	Standley 15191 (US)
	W. oregana D.C. Eaton	*Woodsia oregana*	*Woodsia oregana* subsp. *oregana*	1934-1954	√	Maguire 16372 (UTC)

[1] whenever the date 1892 is listed in this column, this refers to the earliest collection of the taxon known from the Park; these were made by R. S. Williams
[2] whenever possible, photographs of observations made in the field in 2019 were posted to iNaturalist (2021) and are listed here according to their unique ID number (*e.g.*, iNaturalist observation ID 87907372 can be found by visiting <inaturalist.org/observations/87907372>).
[3] verified and annotated by D.M. Brunton in 2004 (pers. comm.)
√ = specimen observed in field in 2019, but without photographic documentation in iNaturalist
— = not applicable

TABLE 2. Lycophyte and fern taxa, either from Lesica (2002) or other sources, for Glacier National Park **not confirmed** in this study. Classes, subclasses, and families are organized phylogenetically following the classification in PPG 1 (2016).

Classification	Taxon name	Information Source(s)
Lycopodiopsida (lycophytes)		
Isoëtaceae	*Isoëtes echinospora* Durieu	Listed in Lesica (2002) based on Maguire's (1939) report of his collection from Trout Lake [*Maguire & Piranian 5429*; GH, UTC] of *I. braunii* Durieu (=synonym of *I. echinospora*). However, GH and UTC specimens annotated as "probably *I. bolanderi*" and "*I. occidentalis*", respectively, by Shackleford (1997).
	I. howellii Engelm.	[*Pierce s.n.* (Glacier National Park Herbarium 23260)]. Herbarium sheet annotated as "*I. howellii* (probably)" by D.M. Brunton in 2004 (pers. comm.).
	I. occidentalis L.F. Henderson	[*Maguire & Piranian 5429*; GH, UTC]. Herbarium sheet at UTC annotated as "*I. occidentalis*" by Shackleford (1997), which is in conflict with his annotation "probably *I. bolanderi*" for the same collection deposited at GH.
Lycopodiaceae	*Diphasiastrum sitchense* (Rupr.) Holub	Lesica (2002). No vouchers confirmed; see Discussion
	Huperzia miyoshiana (Makino) Ching	Lesica (2002). No vouchers confirmed; see Discussion
	Lycopodium clavatum L.	Lesica (2002). No vouchers confirmed; see Discussion
Polypodiopsida (ferns) Equisetidae		
Equisetaceae	*Equisetum* × *litorale* Kühlew. ex Rupr. *(arvense* × *fluviatile)*	Lesica (2002). No vouchers confirmed; see Discussion
	E. palustre L.	Lesica (2002). No vouchers confirmed; see Discussion
Polypodiopsida (ferns) Ophioglossidae		
Ophioglossaceae	*Botrychium angustisegmentum* (Pease & A.H. Moore) R.T. Clausen	Lesica (2002). No vouchers confirmed; see Discussion

Methods) was crucial, both for identifying species with clear macromorphological differences and locating specimens of cryptic taxa that could be obtained on loan. Another factor driving the increase in species numbers in the Park, especially in the years since publication of Lesica's (2002) flora, is the recognition of taxa new to science. Intensified systematic and phylogenetic

research using molecular tools developed in the late 1900s and early 2000s has led to the recognition of several new species, particularly within *Botrychium*.

Among ferns and lycophytes, the leptosporangiate ferns are usually more visible and straightforward to identify than the eusporangiate ferns (Equisetaceae and Ophioglossaceae), or the lycophytes (Isoëtaceae, Lycopodiaceae, and Selaginellaceae). Of the 25 leptosporangiate ferns that we confirm here for the Park (Table 1), 20 were relocated by the lead author in the summer of 2019. Three of the "missing" taxa—*Cystopteris montana*, *Dryopteris cristata*, *Polystichum andersonii*—are quite distinctive morphologically, and the failure to relocate these species is a direct reflection of their rarity. The other two leptosporangiate ferns confirmed for the Park but not relocated in 2019 are *Gymnocarpium dryopteris* and *G.* × *brittonianum*—in addition to being rare in the region, both are difficult to distinguish in the field from the much more common *G. disjunctum* (Pryer and Haufler, 1993).

Our success rate in the field survey was much lower with lycophytes and eusporangiate ferns, which often require specialized knowledge of microscopic and cryptic characters for accurate identification. The lead author was able to relocate just under a third of these (13 out of 46) in his 2019 field survey. In this case, most of the taxa not found in our survey belong to the genus *Botrychium* in the Ophioglossaceae (Table 1). Their ephemeral nature, largely subterranean life cycle, diminutive size, and simple morphology make these plants particularly difficult to find and identify in the field. A proclivity for the production of allopolyploid taxa, derived through hybridization and therefore morphologically intermediate between their diploid parents, further compounds this problem (Dauphin *et al.*, 2018; Farrar *et al.*, 2017).

To supplement the information summarized in Tables 1 and 2, we provide further discussion below on each of the fourteen fern and lycophyte families known to occur in the Park. The families are organized phylogenetically following the classification in PPG 1 (2016).

Lycopodiaceae.—This is the third most diverse family in the fern and lycophyte flora of Glacier National Park (Table 1). We confirm the occurrence of eight species and one interspecific hybrid distributed among four genera: *Dendrolycopodium, Diphasiastrum, Huperzia,* and *Lycopodium s.s.* By contrast, Standley (1920) listed six taxa (all included in *Lycopodium s.l.*) and Lesica (2002) reported ten species assigned to three genera. The generic taxonomy of the Lycopodiaceae has changed radically in recent years in light of a growing body of molecular data (see Øllgaard, 2012, 2015; PPG 1, 2016). Although it has become common practice to place the Park species herein called *Lycopodium annotinum* in the segregate genus *Spinulum* A. Haines, molecular phylogenetic analyses by Field *et al.* (2016) indicate that this species is sister to *Lycopodium s.s.*, and we favor maintaining these two small clades as a single genus with a shared chromosome base number of $x = 34$.

Three lycopods, *Dendrolycopodium dendroideum*, *Diphasiastrum complanatum*, and *Lycopodium annotinum* are among the earliest documented collections from the area, all taken in 1892 by R. S. Williams, one of the earliest field naturalist explorers in Montana (Steere, 1945). These are common in the

Park, and all three were observed during our 2019 resurvey (Table 1). Standley (1920) reported three additional taxa in the genus *Lycopodium*: *L. alpinum, L. clavatum monostachyon,* and *L. selago*. The first of these, now known as *Diphasiastrum alpinum*, is relatively common and well documented by a series of collections between 1919 and 2009 (Table 1). The taxon Standley (1920) referred to as *L. clavatum monostachyon* is now treated as a distinct species, *Lycopodium lagopus* (Wagner and Beitel, 1993); this taxon appears to be rare though documented by several collections between 1919 and 1985. With regard to *Lycopodium selago*, this name has been broadly applied in the past to a diversity of species now included in the genus *Huperzia* (see Bjork, 2020 and references therein). Specimens originally identified as *L. selago* by Standley (1920) have mostly malformed spores and appear to represent a hybrid between *Huperzia continentalis* and *H. occidentalis* (see Testo, Haines, and Gilman, 2016). Nevertheless, *Huperzia selago* sensu Testo, Haines, and Gilman (2016) has been collected in the Park (Table 1), where it appears to be very rare and confined to fen habitats.

Lesica (2002) recorded several additional taxa of Lycopodiaceae from the Park that are not on our list of accepted names (Table 1). Following the taxonomy of Wagner and Beitel (1993), Lesica (2002) reported *Huperzia haleakalae* from the Park. Testo, Haines, and Gilman (2016) restricted this name to populations endemic to Hawai'i and renamed the continental North American taxon *H. continentalis*; they specifically cite a collection from the Park (*Barkley 1735,* WTU) as a representative specimen (Table 1). Three other Lycopodiaceae taxa reported for the Park by Lesica (2002) appear on our unconfirmed list (Table 2). To date, we have seen no specimens attributable to *Diphasiastrum sitchense*; all collections identified as such appear to represent the closely similar species *D. alpinum*. Although there are a few herbarium collections from Montana that have been identified as *Huperzia miyoshiana*, none of them are morphologically identical to confirmed collections from the wet forests of the Pacific Northwest. Overall, these Montana collections more closely resemble *H. occidentalis*, a name that has been applied to most of them in the past and that we adopt here (Table 1). None of the major resources used to distinguish North American *Huperzia* species (*e.g.*, Gilman and Testo, 2015; Testo, Haines, and Gilman, 2016; Wagner and Beitel, 1993) attribute *H. miyoshiana* to Montana. Finally, we have seen no specimens of *Lycopodium clavatum s.s.* gathered within Park boundaries (Table 2); local collections belonging to the *L. clavatum* species complex produce a single strobilus per peduncle, indicating that they represent the segregate taxon *L. lagopus* (called *L. clavatum monostachyon* by Standley in 1920; see Table 1).

Isoëtaceae.—This family includes a single extant genus with more than 200 species (PPG 1, 2016). Although seemingly suitable aquatic habitats are common in the Park, Standley (1920) did not encounter *Isoëtes* during his fieldwork. Lesica (2002) reported both *I. bolanderi* and *I. echinospora* to be locally common, but most local *Isoëtes* collections lack the megaspores needed to unequivocally distinguish these species. The lead author investigated several promising habitats during his 2019 field survey but failed to relocate

any plants of *Isoëtes*. The Glacier National Park herbarium, which is not digitized or available online, does have a single fertile specimen of *Isoëtes bolanderi* collected in 1994 (Table 1) whose identification was verified by Daniel Brunton in 2004 (pers. comm.). Three populations of *I. bolanderi* are known in nearby Canada, all from a small area in Waterton Lakes National Park in southern Alberta (Achuff *et al.*, 2011; Brunton *et al.*, 2020). One of these is within a few hundred meters of the US border.

Another *Isoëtes* collection we examined was *Maguire & Piranian 5429* from Trout Lake. Originally identified as *I. braunii* Durieu (=*I. echinospora*) by Maguire (1939), it is represented by two sterile sheets deposited at GH and UTC. Although likely conspecific, these were annotated as "probably *I. bolanderi*" and "*I. occidentalis*", respectively, by Shackleford (1997), as part of an unpublished PhD dissertation from Miami University. The latter taxon is thus included in our list of unconfirmed reports (Table 2), along with *I. echinospora*, which occurs in and around nearby Flathead Lake, but apparently has not been documented from the Park. Finally, a specimen in the Glacier National Park Herbarium, collected by J. R. Pierce in 1999, was annotated as "*I. howellii* (probably)" by Daniel Brunton in 2004 (pers. comm.; Table 2). A recent paper by Brunton *et al.* (2020) suggests that *I. howellii* may be a low-elevation subspecies of *I. bolanderi*. Clearly, the taxonomy of *Isoëtes* in Glacier National Park is in need of further study.

Selaginellaceae.—As commonly circumscribed (*e.g.*, PPG 1, 2016), this family includes a single extant genus encompassing more than 700 species, most of which occupy tropical and subtropical habitats. For Glacier National Park, we confirm the occurrence of two species (*Selaginella densa* and *S. wallacei*), the same two reported in 1920 by Standley (Table 1). Shortly after Standley's botanical survey of the Park (and based largely on his collections), Maxon (1920, 1921) split *S. densa* into three taxa (*densa, scopulorum,* and *standleyi*) that he treated as species. However, as pointed out by Tryon (1955), these taxa are completely intergradient in the central and southern Rocky Mountains. Therefore, we follow Tryon's taxonomic treatment, recognizing these three entities as varieties, all of which occur within the boundaries of Glacier National Park. Lesica (2002) reported three species of *Selaginella* from the Park (*S. scopulorum, S. standleyi*, and *S. wallacei*), apparently overlooking the fact that the largely High Plains taxon *S. densa s.s.* (our var. *densa*) had been collected by Standley in 1919 within the eastern border of the Park (Table 1). This area was not revisited during the 2019 field survey and the search for var. *standleyi* was ultimately unsuccessful (no documented vouchers since 1949; Table 1). However, the two more common taxa with more extensive collection histories (*S. densa* var. *scopulorum* and *S. wallacei*) were both observed in 2019.

Equisetaceae.—This ancient family comprises a single extant genus (*Equisetum*) with about 15 surviving species (Christenhusz *et al.*, 2019; Des Marais *et al.*, 2003; PPG 1, 2016). Glacier National Park is a major center of diversity for the group, with eight fertile species and two sterile hybrids on our list of confirmed taxa (Table 1). These taxa represent two deeply divergent

subgenera (*Equisetum* and *Hippochaete*) that are occasionally treated as genera (Farwell, 1916; Milde, 1865). Four of the fertile species belong to subg. *Equisetum* (Christenhusz *et al.*, 2019; Hauke, 1978); three of these (*E. arvense, E. fluviatile*, and *E. sylvaticum*) were relocated during the 2019 field season, with *E. arvense* clearly being the most common fern in the Park. The fourth member of subg. *Equisetum* confirmed for the Park (*Equisetum pratense*) was not encountered by Standley (1920), but several herbarium specimens obtained on loan for our project support Lesica's (2002) report.

The remainder of the *Equisetum* species confirmed for the Park (four fertile species and two sterile hybrids) belong to subg. *Hippochaete* (Christenhusz *et al.*, 2019; Hauke, 1963). *Equisetum hyemale* subsp. *affine*, *E. laevigatum,* and *E. variegatum* subsp. *variegatum* are all common in appropriate habitats and were relocated by the lead author in 2019 (Table 1); the presence of *E. scirpoides,* a rarer taxon not reported by Standley (1920), was confirmed from herbarium specimens we obtained on loan. Much of the nomenclatural confusion apparent in this group relates to the presence of two sterile, interspecific hybrids: *E.* × *ferrissii* (*E. hyemale* × *E. laevigatum*) and *E.* × *trachyodon* (*E. hyemale* × *E. variegatum*). Lesica (2002) did not mention these hybrids, and Standley (1920) did not recognize them as such although he collected both. The collection Standley published as "*E. praealtum*" is *E.* × *ferrissii*, as is one of the specimens he identified as *E. variegatum*. Standley also collected *E.* × *trachyodon*, but attributed the specimen to *E. variegatum,* one of this hybrid's parental taxa.

The fern that has possibly expanded its already large range the most in the last 100 years is *Equisetum arvense*. Standley (1920) noted that it was "common, and often abundant, at all elevations except the highest . . . it seems to thrive particularly well on railroad embankments, and a thick stand of the plants is often seen growing from dry gravel and cinders". With the proliferation of vehicular traffic since Standley's writing, there are now miles of new roads throughout the Park, where, lined up in the ditches on either side, grow carpets of *E. arvense*. Found in all vegetation zones (Lesica, 2002), almost everywhere the soil has been disturbed—be it along a creek or in the headquarters gravel parking lot in West Glacier—one can expect to find shoots of *E. arvense* ready to colonize another territory.

Two taxa of subg. *Equisetum* (*E. palustre* and *E.* × *litorale*) appear on our unconfirmed list (Table 2). Online images of specimens from the Park attributed to *E. palustre* do not represent a single taxon, and we are unable to resolve the situation without more detailed analyses of microscopic features. Regarding *E.* × *litorale,* specimens identified as such by Standley (1920) were later annotated by R. L. Hauke as *E. arvense*, in conjunction with his monograph on *Equisetum* subg. *Equisetum* (Hauke, 1978). Collections attributed to *E.* × *litorale* by Lesica (2002) have partially malformed spores suggesting that they may be hybrids between different species of subg. *Equisetum*. However, these plants are not a good match for *bona fide* specimens of *E. arvense* × *E. fluviatile* (the hypothesized parentage of *E.* × *litorale*; Hauke, 1978). Given the diversity of potential parents in the Park (and

the possibility that the spore abortion is due to environmental factors rather than hybridization), we cannot unequivocally assign these specimens to *E.* × *litorale*.

Ophioglossaceae.—As circumscribed by PPG 1 (2016), this family comprises four subfamilies, two of which are present in Glacier National Park. The Ophioglossoideae are represented in the Park by a single species, *Ophioglossum pusillum*, which is apparently confined to fen habitats and is quite rare, having been collected just once in 1993 (Table 1). By contrast, the Botrychioideae, is the most diverse fern lineage in the Park, including 19 species and two hybrids (Table 1). Standley (1920) recognized just three species belonging to Botrychioideae among his collections from Glacier National Park: *Botrychium lunaria, B. silaifolium*, and *B. virginianum*. The clear morphological differences among these three taxa were acknowledged in past classifications by their assignment to different subgenera (Clausen, 1938; Wagner and Wagner, 1993), and recent molecular phylogenetic analyses reveal that these groups are deeply divergent (Zhang *et al.*, 2020). As a result, it has become common practice in the two decades since publication of the *Flora of Glacier National Park, Montana* (Lesica, 2002) to place these species in different genera (see PPG 1, 2016). Collections identified as *Botrychium silaifolium* by Standley (1920) and *B. multifidum* by Lesica (2002) are herein called *Sceptridium multifidum*, and the specimens previously assigned to *Botrychium virginianum* are treated as *Botrypus virginianus*. Both are relatively common in the Park, with a long history of documentation extending from 1901 to the 2019 field studies of the lead author (Table 1).

Plants of the genus *Botrychium s.s.* make up the most diverse group of ferns within Glacier National Park, with seventeen species and two hybrids recognized (Table 1). Members of *Botrychium* are morphologically quite simple, comprised of a single underground stem and roots, and a single leaf produced above ground in a given year. The leaf is branched into two segments, a skeletonized sporophore producing spores, and a once or twice pinnate blade called the trophophore. Because this basic structure is common to all *Botrychium*, they are extremely difficult to distinguish by morphology alone and have often been called "cryptic" species (Dauphin *et al.*, 2017). Their relatively small size and frequent occurrence within dense native perennial herbaceous vegetation makes them difficult to find.

Recognition of the true diversity within *Botrychium* has been relatively recent. In his 1938 monograph of the genus (then recognized as subgenus *Eubotrychium*), Clausen listed just six species worldwide, with only *B. lunaria* reported for Glacier National Park. A few additional taxa were described over the next half-century, but the recognition of new species accelerated greatly when cytological studies revealed that roughly half of *Botrychium* taxa were allopolyploids. These new data, plus more critical morphological examination, led W. H. and F. S. Wagner to describe 16 new species from North America between 1956 and 2002 (*e.g.*, Wagner and Grant, 2002; Wagner and Lord, 1956). Subsequently, the documentation of genetic markers unique to individual taxa further substantiated identities of previously described

diploids, and also revealed the diploid parents of allopolyploids (Gilman, Farrar, and Zika, 2015; Zika and Farrar, 2009). The advancement of these new techniques allowed Farrar and coworkers to distinguish even more morphologically cryptic species, especially within what was previously considered a single, worldwide species, *B. lunaria*. Stensvold and Farrar (2016) now recognize five diploid and one allotetraploid taxa within the *B. lunaria* complex (Dauphin *et al.*, 2017, 2018). Although *B. lunaria* was listed by both Standley (1920) and Lesica (2002) as being present in the Park (Table 1), its revised circumscription now excludes it. Continuing investigations of *Botrychium* now estimate the total number of taxa in the genus to be close to 40.

Glacier National Park has played a prominent role in the discovery of new *Botrychium* taxa and understanding their evolutionary origins. *Botrychium lineare*, now considered a variety of *B. campestre* (Table 1; Farrar and Gilman, 2017), was initially thought to be extremely rare and placed on the federal candidate endangered species list—until hundreds of plants were discovered in the Park (Barton and Crispin, 2004; Farrar and Gilman, 2017). *Botrychium* × *watertonense*, still known only from Glacier and the adjoining Waterton Lakes National Park in Canada, is the only known allopolyploid species that combines genomes from four different diploid species (Wagner *et al.*, 1984). Furthermore, analysis of plastid DNA shows *B.* × *watertonense* to have originated independently in these two known sites (Dauphin *et al.*, 2017). The rare taxon, *B. gallicomontanum*, basically an "eastern US" species, was surprisingly found in western prairies of the park (Popovich and Farrar, 2020). Also in the same prairies, was an enigmatic species found by Peter Lesica in 1996 and informally named *B.* "*adnatum*" by W. H. Wagner in 1998. The mystery of no additional discoveries of "*adnatum*" was not resolved until 2005, when it was found to be genetically identical to a Rocky Mountain taxon considered by W. H. Wagner to be a western form of *B. pallidum*. But although containing a genome of *B. pallidum* (and thus its similar morphology), "*adnatum*" and "*western pallidum*" plants proved to be an allotetraploid taxon with parentage by *B. pallidum* and an undescribed new diploid species. This widespread allopolyploid, now known from southern Canada to New Mexico, was named *B. furculatum* by Popovich & Farrar in 2020 (Table 1).

Are additional *Botrychium* yet to be discovered in Glacier National Park? With its wide range of habitats, from mountain meadows to native prairies, both favored by *Botrychium*, the answer is most likely yes! *Botrychium neolunaria*, the common North American species of the *B. lunaria* complex, is curiously absent from the Park. Farrar and colleagues collected 44 plants from six different sites in the Park, all with a morphology similar to *B. neolunaria,* however, genetic analyses proved them all to be an allotetraploid, *B. yaaxudakeit,* derived from hybridization between *B. neolunaria* and a North American form of *B. lunaria*. *Botrychium yaaxudakeit* is common from Alaska to southwestern Canada and disjunct to Oregon and California. *Botrychium neolunaria* can be distinguished from *B. yaaxudakeit* by its thinner, lighter-

green leaflets and significantly smaller spores (37μ vs. 45μ), and we anticipate that it will one day be found in the Park.

Of current interest is the newly discovered diploid species *B. farrarii* ined., one of the parents of *B. furculatum* discussed above. *Botrychium* "*farrarii*" is currently known only from the Big Horn Mountains of northern Wyoming. The westernmost occurrence of the other diploid parent of *B. furculatum*, *B. pallidum*, is in the Bearlodge Mts. in northeastern Wyoming. For allopolyploid hybridization to have occurred between these two species they must have cohabited the same site at some time. Because allotetraploids *B. furculatum* and *B. gallicomontanum* occur in the prairies of western Glacier National Park (Table 1), and both share *B. pallidum* as a parent, it is intriguing to ask whether *B. pallidum* might still be found in these prairies. Might *B.* "*farrarii*" be there as well? In any case, Glacier National Park seems to have been an evolutionary hotbed for the generation of allopolyploids, which comprise 61% (11 of 19) of the *Botrychium* species in the Park.

Pteridaceae.—In Glacier National Park, this family is represented by five species currently assigned to four genera (Table 1). All are relatively common, and each has a long history of documentation extending from the late 1800's to their observation during our 2019 field survey (Table 1). The taxonomy of the two *Cryptogramma* species has remained unchanged since they were first reported for the Park (see Metzgar *et al.*, 2013), and the separation of the western North American populations of the *Adiantum pedatum* complex at varietal (Standley, 1920) or species level (*Adiantum aleuticum* in Huiet *et al.*, 2018; Lesica, 2002; Paris, 1991) also has stood the test of time. The most significant changes in the nomenclature of local Pteridaceae arise from the incremental exclusion of the genus *Cheilanthes* from the floristic inventory. The species referred to as *Cheilanthes siliquosa* by Standley (1920) was recognized as *Aspidotis densa* by Lellinger (1968) and Lesica (2002). Subsequent molecular phylogenetic analyses supported this move, indicating that this taxon is deeply divergent from *Cheilanthes s.s.* and sister to the genus *Gaga* (Li, Pryer, and Windham, 2012). In fact, a series of such studies over the past decade (Eiserhardt *et al.*, 2011; Grusz *et al.*, 2014; Ponce and Scataglini, 2018) has shown that none of the North American species attributed to *Cheilanthes* are appropriately placed in this genus. As typified by *C. micropteris* Sw., *Cheilanthes s.s.* comprises a clade of about 30 species found almost exclusively in the Southern Hemisphere. It is deeply diverged from the clade that includes the Glacier National Park species formerly known as *C. gracillima* and, as such, the latter has been transferred to the genus *Myriopteris* (along with ca. 45 closely related North American taxa; see Grusz and Windham, 2013).

Dennsteadtiaceae.—A single species belonging to this family is known from Glacier National Park—the very widespread *Pteridium aquilinum*—which was frequently encountered west of the Continental Divide in our 2019 field survey (Table 1). Collections from the area have been identified as either var. *pubescens* Underw. or, less frequently, var. *latiusculum* Desv. We have examined all specimens attributed to the latter and find that none of them

match the current circumscription of this taxon. Therefore, we assign all specimens of *Pteridium* from the Park to *P. aquilinum* subsp. *pubescens* following the taxonomy of Thomson, Mickel, and Mehltreter (2008).

Cystopteridaceae.— This family has a complex nomenclatural history; in the past two decades it has been placed in synonymy under either Dryopteridaceae (*e.g.*, Lesica, 2002) or Woodsiaceae (Smith *et al.*, 2006). Its recognition as a distinct family with ca. 40 species is strongly supported by recent molecular phylogenetic studies (PPG 1, 2016; Rothfels *et al.*, 2012; Rothfels, Windham, and Pryer, 2013). The family is represented in the Park by two species of *Cystopteris* and two species and an interspecific hybrid belonging to *Gymnocarpium* (Table 1). The two *Cystopteris* taxa are at opposite ends of the spectrum in terms of abundance; *C. fragilis* subsp. *fragilis* is one of the most common ferns in the area (and the world) whereas *C. montana* is an arctic-alpine specialist collected from the Park just once, in 1932 (Table 1). *Cystopteris fragilis* subsp. *fragilis* is morphologically and cytologically diverse in Glacier, comprising tetraploid and hexaploid populations that hybridize to form heterotic but sterile pentaploids (Windham, pers. obs.). This situation is remarkably similar to that reported from comparable latitudes in Eurasia (Hanušová *et al.*, 2019).

The three *Gymnocarpium* taxa occurring in Glacier National Park also differ greatly in abundance. Most collections from the area (>90%) represent the Pacific Northwest diploid species *G. disjunctum*. The circumboreal allotetraploid *G. dryopteris*, which originated through hybridization between *G. disjunctum* and the rare eastern North American species *G. appalachianum* (Pryer and Haufler, 1993; Rothfels *et al.*, 2014), has rarely been collected in the Park. In fact, this species appears to be even rarer than its sterile triploid backcross with *G. disjunctum* (= *G.* × *brittonianum*), whose previously unreported presence was confirmed based on several herbarium specimens obtained on loan. Although the spores of *G.* × *brittonianum* are largely malformed, many plants produce a few unreduced spores that may allow the hybrid to establish new sporophytes via apomixis (Pryer and Haufler, 1993).

Aspleniaceae.—This family is represented in the Park by a single species (Table 1) belonging to the cosmopolitan *Asplenium trichomanes* L. clade (Xu *et al.*, 2020). For two centuries, this circumboreal taxon was known as *Asplenium viride*, the name used by Standley (1920). A competing name (*A. trichomanes-ramosum* L.) emerged from taxonomic obscurity in the late 20th century and was adopted by both the *Flora of North America* (Wagner, Moran, and Werth, 1993) and the *Flora of Glacier National Park, Montana* (Lesica, 2002). However, *Asplenium trichomanes-ramosum* is now considered invalid (nom. inval., see ICBN Art. 56 and ICBN Appendix V (nom. utique rejic.) under *Asplenium ramosum*, Vienna Code, McNeill *et al.*, 2006) and we here return to the legitimate name *A. viride*, which has been conserved over all other names. This species, first documented for the area in 1901, is relatively common and was observed in several places during our 2019 field season.

Thelypteridaceae.—This family is represented in Glacier National Park by a single taxon, *Phegopteris connectilis* (Table 1). The first collections of this

species in the Park were apparently made by Marcus Jones in 1909. However, perhaps due to a combination of rarity and difficult access, it was not encountered by Standley (1920). Most collections come from the vicinity of Sperry Glacier (Lesica, 2002), whose remote location (8.7 trail miles from the nearest road) discourages all but the most intrepid botanists. Despite these challenges, the lead author was successful in relocating this distinctive species in 2019 (Table 1). *Phegopteris* and its close relatives (the phegopteroid lineage) diverged early in the evolutionary history of the Thelypteridaceae, and the generic boundaries in this group are relatively stable and widely accepted compared to those in the rest of the family (Almeida *et al.*, 2016).

Phegopteris connectilis is unique among the Park's ferns in being an apomictic triploid that produces mostly unreduced spores, which germinate to form triploid gametophytes that, in turn, give rise to new sporophytes without fertilization (Patel, Fawcett, and Gilman, 2019). This trait is most commonly found in species that occupy drought-prone habitats (Grusz *et al.*, 2021), and it is very unusual to see it so well developed in a mesic species like *P. connectilis*. Unreduced spores have been observed in two other ferns occurring in the Park: *Gymnocarpium* × *brittonianum* (= diploid *G. disjunctum* × tetraploid *G. dryopteris*; Pryer and Haufler, 1993) and *Huperzia continentalis* × *occidentalis* (Testo, Haines, and Gilman, 2016). These two hybrids regularly form discrete populations in the absence of one or both parents, suggesting they may be experiencing incipient apomixis. The origin of triploid *Phegopteris connectilis* has not been ascertained, but hybridity has not been ruled out (Patel, Fawcett, and Gilman, 2019). Thus, hybrid origins (and possibly triploidy) may be driving the evolution of apomixis in all three of these mesic lineages.

Woodsiaceae.—As defined by PPG 1 (2016), this family includes two species found in Glacier National Park; both of which were relocated by the lead author in 2019 (Table 1). The circumscription of Woodsiaceae has changed substantially since its resurrection by Smith *et al.* (2006); with the removal of Athyriaceae, Cystopteridaceae, and several small, mostly tropical families (Rothfels *et al.*, 2012), Woodsiaceae now comprises a monophyletic group of about 40 species. Despite the low number of extant taxa, some of the internal clades are deeply divergent and, as a result, the generic taxonomy of the family has become a point of contention. Where PPG 1 (2016) accepts a single genus of Woodsiaceae, Lu *et al.* (2019) recognizes three (including a hybrid nothogenus), and Shmakov (2015) proposes seven.

Depending on the generic scheme adopted, the species of Glacier National Park belong to either *Woodsia* (PPG 1, 2016), *Physematium* (Lu *et al.*, 2019), or *Woodsiopsis* (Shmakov, 2015). Recent molecular phylogenetic analyses with broad sampling of Woodsiaceae (Larsson, 2014; Lu *et al.*, 2019) indicate that *Woodsiopsis* and *Physematium sensu* Shmakov (2015) are non-monophyletic, and adoption of this scheme would require the placement of the two Glacier National Park species in separate genera. Because hybridization occurs between the deepest branches in the Woodsiaceae phylogeny, the recognition of two or more genera also requires the naming of hybrid nothogenera (Lu *et*

al., 2019). Here we follow the single genus classification of Woodsiaceae (PPG 1, 2016), assigning both local taxa to the genus *Woodsia*. One of these (*W. scopulina* subsp. *scopulina*) is cytologically diverse in the Park, including both diploid and tetraploid populations distinguished primarily by spore size (Windham, pers. obs.). The exclusively diploid taxon from the Park previously identified as *W. oregana* subsp. *oregana* by Lesica (2002) is herein referred to simply as *W. oregana*. Molecular phylogenetic analyses by Larsson (2014) have shown that tetraploid plants formerly classified as subsp. *cathcartiana* (Windham 1993a, 1993b) are allopolyploids deserving of species rank.

Athyriaceae.—This family has a complex nomenclatural history; in the past two decades it has been placed in synonymy under either Dryopteridaceae (*e.g.*, Lesica, 2002) or Woodsiaceae (Smith *et al.*, 2006). Its recognition as a distinct family with ca. 650 species (PPG 1, 2016) is strongly supported by recent molecular phylogenetic studies (Rothfels *et al.*, 2012). The family is represented in the Park by two circumboreal species—*Athyrium distentifolium* and *A. filix-femina*—first collected in the 1890's and easily relocated during our 2019 field survey (Table 1). The Glacier National Park taxon here called *A. distentifolium* subsp. *americanum* has also been treated as a variety of *A. alpestre* (Lesica, 2002) or a distinct species (Standley, 1920); it differs from the typical European taxon in lacking even a vestigial indusium. In recent molecular phylogenetic analyses of Athyriaceae (Wei *et al.*, 2018), *A. alpestre* was well supported as sister to the small segregate genus *Cornopteris* Nakai; this branch was, in turn, sister to *Athyrium s.s.* (typified by the other Glacier species, *A. filix-femina*). To establish monophyly in this portion of the phylogenetic tree, Wei *et al.* (2018) advocated placing *A. alpestre* in the monospecific genus *Pseudathyrium* Newman. Alternatively, *A. alpestre* can be maintained in *Athyrium* (as *A. distentifolium*) if *Cornopteris* is also included. Because *A. distentifolium* hybridizes with the type species of *Athyrium* (Schneller, 1989), we follow PPG 1 (2016), which includes this species in *Athyrium s.l.* It should also be noted that *A. filix-femina* is highly variable across its range, and local populations belong to the Pacific Northwest segregate known as var. or subsp. *cyclosorum*.

Dryopteridaceae.—In the narrow sense adopted by PPG 1 (2016), this family is represented in the Park by seven species, four belonging to the genus *Dryopteris* and three to *Polystichum* (Table 1). Standley (1920) also reported four species of *Dryopteris* from Glacier National Park, and the names of two of these remain unchanged. The taxon that Standley (1920) called *D. linnaeana* has since been removed from the genus and, more recently, the family as well (Rothfels *et al.*, 2012). This name is a synonym of *Gymnocarpium dryopteris*, though the specimens collected and examined by Standley belong to the closely related species *G. disjunctum* (see discussion of Cystopteridaceae).

The collections identified by Standley (1920) as *Dryopteris dilatata* (Hoffm.) A. Gray were subsequently shown to represent two species, a diploid (*D. expansa*) and a circumboreal allotetraploid (*D. carthusiana*). The latter is thought to be a hybrid between two species (*D. intermedia* and the still hypothetical *D. semicristata*) not known to occur in western North America

(Sessa, Zimmer, and Givnish, 2012). Although the distinctions between *D. carthusiana* and *D. expansa* are subtle, they do not appear to hybridize in nature (Montgomery and Wagner, 1993). Three of the four species of *Dryopteris* confirmed for the Park (Table 1) are relatively abundant and were easily relocated in 2019 (Table 1). *Dryopteris cristata*, on the other hand, has only been collected in the vicinity of John's Lake in the McDonald Valley. Three separate trips to this small fen by the lead author in 2019 failed to relocate this species; the last collection from the Park dates to 2000 (Table 1).

Standley (1920) reported two species of *Polystichum* (*P. andersonii* and *P. lonchitis*) for Glacier National Park, and Lesica (2002) added *P. munitum* to the list (Table 1). The three taxa do not appear to be closely related based on molecular phylogenetic analyses (Driscoll and Barrington, 2007; Le Péchon *et al.*, 2016). *Polystichum lonchitis* is relatively common in the Park and was observed at several locations by the lead author in 2019. *Polystichum andersonii* was not relocated during the 2019 field season, but herbarium specimens seen online confirm its presence in the Park. Although all online images of *P. munitum* herbarium specimens from the area proved to be misidentified collections of *P. lonchitis*, there is a confirmed voucher for *P. munitum* in the Glacier National Park Herbarium collected by Spribille in 1994, and it was also observed in 2019 (Table 1).

Polypodiaceae.—In the narrow sense adopted by PPG 1 (2016), this family is represented in Glacier National Park by a single species, *Polypodium hesperium*. First collected in the Park in 1900, the nomenclature of this taxon has remained largely unchallenged for more than a century. Although uncommon, the species is easily distinguished from other members of the local fern flora and was relocated during our 2019 survey (Table 1). *Polypodium hesperium* is a tetraploid that arose through hybridization between two Pacific Northwest diploids (*P. amorphum* Suksd. and *P. glycyrrhiza* D.C. Eaton) and then spread south (to Chihuahua, Mexico) and east (to Glacier National Park) exploiting new habitats seemingly unavailable to its parental species (Sigel, Windham, and Pryer, 2014).

Conclusions

What has changed in Glacier National Park in the past 130 years? Visitation has steadily increased, from 19,000 tourists in 1919 to more than 3 million in 2019 (National Park Service, 2020). Facilitating this growth has been the construction of roads, campgrounds, and parking lots, allowing people access to previously remote wilderness areas. Well established hiking trails (>700 miles) now crisscross the Park. Less noticeable but just as impactful are recent climatic changes and their effects on the glaciers that are the hallmark of the area. Since 1900, average air temperatures in the Park have increased by 1.33 degrees Celsius (Pederson *et al.*, 2010), and the number and size of glaciers has drastically declined. Shifting climate patterns are known to affect plant distributions and population sizes, especially for those on the edge of their ranges (Lesica *et al.*, 2018). This

suggests that as glaciers continue to shrink, the diminished snowmelt may impact fern and lycophyte diversity. Despite these alterations to the landscape, 95% of the Park remains a protected wilderness that has seen relatively limited human-mediated impacts (Lesica, 2002). This is reflected in the current inventory of ferns and lycophytes for the Park. Nine taxa attributed to the Park by various sources in the last 130 years (*e.g.*, Lesica, 2002, herbarium specimen annotations) remain unconfirmed (Table 2). Most of these belong to taxonomically difficult groups that require observation of cryptic characters for positive identification. Even with these deletions (some of which may be reversed by further studies), the 71 ferns and lycophytes confirmed here for Glacier National Park represent a substantial increase over the 61 reported by Lesica (2002). This is due, in large part, to intensified systematic and phylogenetic research focused on certain groups (most notably the genus *Botrychium*). Climatic changes over the next century will certainly contribute in unknown ways to the evolving dynamics of ferns and lycophytes within the Park over the coming years. However, from the perspective of the fern and lycophyte flora, it is clear that the stewardship and management of Glacier National Park by the National Park Service over the last 110 years has been exemplary, and that this region still merits its early nickname "The Crown of the Continent".

Literature Cited

Achuff, P., C. Bradley, D. F. Brunton, D. Casimir, T. Kemper, and C. Smith. 2011. Recovery strategy and action plan for Bolander's Quillwort (*Isoëtes bolanderi*), in Canada. Parks Canada Agency, Ottawa, Ontario, Canada. Accessed 3 Jan 2021. http://publications.gc.ca/collections/collection _ 2011/pc/En3–4–97–2011–eng.pdf.

Almeida, T. E., S. Hennequin, H. Schneider, A. R. Smith, J. A. N. Batista, A. J. Ramalho, K. Proite, and A. Salino. 2016. Towards a phylogenetic generic classification of Thelypteridaceae: additional sampling suggests alterations of neotropical taxa and further study of paleotropical genera. Molecular Phylogenetics and Evolution 94:688–700.

Barton, D. and S. Crispin. 2004. Conservation status of *Botrychium lineare* (slender moonwort) in Montana. Report to the US Fish and Wildlife Service. Montana Natural Heritage Program, Helena, MT. 16 pp. plus appendices.

Bjork, C. R. 2020. Notes on the Holarctic species of *Huperzia* (Lycopodiaceae), with emphasis on British Columbia, Canada. Annales Botanici Fennici 57:255–278.

Brunton, D. F., M. A. Krichbaum, R. S. Krichbaum, and P. C. Sokoloff. 2020. Distribution and status of Howell's Quillwort (*Isoëtes howellii*, Isoëtaceae) in Canada and its relation to Bolander's Quillwort (*Isoëtes bolanderi*). Canadian Field Naturalist 134:252–264.

Christenhusz, M. J. M., L. Bangiolo, M. W. Chase, M. F. Fay, C. Husby, M. Witkus, and J. Viruel. 2019. Phylogenetics, classification and typification of extant horsetails (*Equisetum*, Equisetaceae). Botanical Journal of the Linnean Society 189:311–352.

Clausen, R. T. 1938. A monograph of the Ophioglossaceae. Bulletin of the Torrey Botanical Club 19:1–177.

Dauphin, B., D. R. Farrar, A. Maccagni, and J. R. Grant. 2017. A worldwide molecular phylogeny provides new insight on cryptic diversity within the moonworts (*Botrychium* s.s., Ophioglossaceae). Systematic Botany 42:620-639.

Dauphin, B., J. R. Grant, D. R. Farrar, and C. J. Rothfels. 2018. Rapid allopolyploid radiation of moonwort ferns (*Botrychium*; Ophioglossaceae) revealed by PacBio sequencing of

homologous and homeologous nuclear regions. Molecular Phylogenetics and Evolution 120:342–353.

Des Marais, D. L., A. R. Smith, D. M. Britton, and K. M. Pryer. 2003. Phylogenetic relationships and evolution of extant horsetails, *Equisetum*, based on chloroplast DNA sequence data (*rbcL* and*trnL-F*). International Journal of Plant Sciences 164:737–751.

Driscoll, H. E. and D. S. Barrington. 2007. Origin of Hawaiian *Polystichum* (Dryopteridaceae) in the context of a world phylogeny. American Journal of Botany 94:1413–1424.

Eiserhardt, W. L., J. G. Rohwer, S. J. Russell, J. C. Yesilyurt, and H. Schneider. 2011. Evidence for radiations of cheilanthoid ferns in the Greater Cape Floristic Region. Taxon 60:1269–1283.

Fagre, D. B., L. A. McKeon, K. A. Dick, and A. G. Fountain. 2017. Glacier margin time series (1966, 1998, 2005, 2015) of the named glaciers of Glacier National Park, MT, USA. US Geological Survey Data Release. doi: 10.5066/F7P26WB1.

Fagre, D. B. and C. J. Martin-Mikle. 2018. A comprehensive inventory of maximum glacial extent in Glacier National Park during the peak of the Little Ice Age: U.S. Geological Survey data release, https://doi.org/10.5066/P95YJ3CN.

Farrar, D. R. and A. V. Gillman. 2017. Relationships in the *Botrychium campestre* (Ophioglossaceae) complex. Brittonia 69:265–275.

Farwell, O. A. 1916. The genus *Hippochaete* in North America, north of Mexico. Memoirs of the New York Botanical Garden 6:461–472.

Field, A. R., W. Testo, P. D. Bostock, J. A. M. Holtum, and M. Waycott. 2016. Molecular phylogenetics and the morphology of the Lycopodiaceae subfamily Huperzioideae supports three genera: *Huperzia, Phlegmariurus*, and *Phyloglossum*. Molecular Phylogenetics and Evolution 94:635–657.

Finklin, A. I. 1986. A climatic handbook for Glacier National Park-with data for Waterton Lakes National Park. General Technical Report INT-204. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Fitzpatrick, T. J. 1904. The fern flora of Montana. Fern Bulletin 12:97–101.

Gilman, A. V. and W. Testo. 2015. Use of gemma characters to identify North American *Huperzia* (Lycopodiaceae). American Fern Journal 105:145–161.

Gilman, A. V., D. R. Farrar, and P. F. Zika. 2015. *Botrychium michiganense* sp. nov. (Ophioglossaceae), a new North American moonwort. Journal of the Botanical Research Institute of Texas 9:295–309.

Grusz, A. L. and M. D. Windham. 2013. Toward a monophyletic *Cheilanthes*: The resurrection and recircumscription of *Myriopteris* (Pteridaceae). Phytokeys 32:49–64.

Grusz, A. L., M. D. Windham, G. Yatskievych, L. Huiet, G. J. Gastony, and K. M. Pryer. 2014. Patterns of diversification in the xeric-adapted fern genus *Myriopteris* (Pteridaceae). Systematic Botany 39:698–714.

Grusz, A. L., M. D. Windham, K. T. Picard, K. M. Pryer, E. Schuettpelz, and C. H. Haufler. 2021. A drought-driven model for the evolution of obligate apomixis in ferns: Evidence from pellaeids (Pteridaceae). American Journal of Botany 108:263–283.

Hall, M. H. P. and D. B. Fagre. 2003. Modeled climate-induced glacier change in Glacier National Park, 1850–2100. BioScience 53:131–140.

Hanušová, K., M. Čertner, T. Urfus, P. Koutecký, J. Košnar, C. J. Rothfels, V. Jarolímová, J. Ptáček, and L. Ekrt. 2019. Widespread co-occurrence of multiple ploidy levels in fragile ferns (*Cystopteris fragilis* complex; Cystopteridaceae) probably stems from similar ecology of cytotypes, their efficient dispersal and inter-ploidy hybridization. Annals of Botany 123:845–855.

Hauke, R. L. 1963. A taxonomic monograph of the genus *Equisetum* subgenus *Hippochaete*. Beihefte zur Nova Hedwigia 8:1–123.

Hauke, R. L. 1978. A taxonomic monograph of *Equisetum* subgenus *Equisetum*. Beihefte zur Nova Hedwigia 30:385–455.

Huiet, L., F.-W. Li, T.-T. Kao, J. Prado, A. R. Smith, E. Schuettpelz, and K. M. Pryer. 2018. A worldwide phylogeny of *Adiantum* (Pteridaceae) reveals remarkable convergent evolution in leaf blade architecture. Taxon 67:488–502.

iNaturalist. 2021. Available from https://www.inaturalist.org. Accessed [08.01.21].

Larsson, A. 2014. Systematics of *Woodsia*: Ferns, bioinformatics and more. Ph.D. dissertation. Uppsala: Acta Universitatis Upsaliensis. http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-232233.

Lellinger, D. B. 1968. A note on *Aspidotis*. American Fern Journal 58:140–141.

Le Péchon, T., H. He, L. Zhang, X.-M. Zhou, X.-F. Gao, and L.-B. Zhang. 2016. Using a multilocus phylogeny to test morphology-based classifications of *Polystichum* (Dryopteridaceae), one of the largest fern genera. BMC Evolutionary Biology 16:55.

Lesica, P. 2002. *Flora of Glacier National Park, Montana*. Oregon State University Press, Oregon.

Lesica, P. 2018. Arctic-alpine plants decline over two decades in Glacier National Park, Montana, U.S.A. Arctic, Antarctic, and Alpine Research 46:327–332.

Li, F.-W., K. M. Pryer, and M. D. Windham. 2012. *Gaga*, a new fern genus segregated from *Cheilanthes* (Pteridaceae). Systematic Botany 37:845–860.

Lu, N. T., X.-M. Zhou, L. Zhang, R. Knapp, C.-X. Li, X.-P. Fan, L. Zhou, H.-J. Wei, J.-M. Lu, B. Xu, Y.-L. Peng, X.-F. Gao, and L.-B. Zhang. 2019. A global plastid phylogeny of the cliff fern family Woodsiaceae and a two-genus classification of Woodsiaceae with the description of × *Woodsimatium* nothogen. nov. Taxon 68:1149–1172.

Maguire, B. 1939. Distributional notes concerning plants of Glacier National Park, Montana. II. Rhodora 41:504–508.

Maxon, W. R. 1920. New Selaginellas from the western United States. Smithsonian Miscellaneous Collections 72:1–10.

Maxon, W. R. 1921. Notes on American ferns—XVII. American Fern Journal 11:33–39.

McNeill J., F. R. Barrie, H.-M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema, and N. J. Turland. 2006. International Code of Botanical Nomenclature (Vienna Code) adopted by the Seventeenth International Botanical Congress Vienna, Austria, July 2005. Regnum Vegetabile 146:1–568; online at https://ibot.sav.sk/icbn/no%20frames/0001Viennatitle.htm.

Metzgar, J. S., E. R. Alverson, S. Chen, A. V. Vaganov, and S. M. Ickert-Bond. 2013. Diversification and reticulation in the circumboreal fern genus *Cryptogramma*. Molecular Phylogenetics and Evolution 67:589–599.

Milde, J. 1865. Repräsentieren die Equiseten der gegenwärtigen Schöpfungsperiode ein oder zwei Genera? Oesterreichische botanische Zeitschrift 23:297–299.

Montgomery, J. D. and W. H. Wagner, Jr. 1993. *Dryopteris*. Pp. 280–288, *in* Flora of North America Editorial Committee (eds.), *Flora of North America North of Mexico. Volume 2. Pteridophytes and Gymnosperms*. Oxford University Press, New York.

National Park Service. 2020. Visitor statistics. https://irma.nps.gov/STATS/SSRSReports/Park%20Specific%20Reports/Park%20YTD%20Version%201?Park=GLAC Retrieved 3 January 2021.

NatureServe. 2021. NatureServe Explorer 2.0 [web application]. NatureServe, Arlington, Virginia. https://explorer.natureserve.org/ Accessed: August 1, 2021.

Øllgaard, B. 2012. New combinations in neotropical Lycopodiaceae. Phytotaxa 57:10–22.

Øllgaard, B. 2015. Six new species and some nomenclatural changes in neotropical Lycopodiaceae. Nordic Journal of Botany 33:186–196.

Page, L. M., B. J. Macfadden, J. A. Fortes, P. S. Soltis, and G. Riccardi. 2015. Digitization of biodiversity collections reveals biggest data on biodiversity. Bioscience 65:841–842.

Paris, C. A. 1991. *Adiantum viridimontanum*, a new maidenhair fern in eastern North America. Rhodora 93:105–121.

Patel, N. R., S. Fawcett, and A. V. Gilman. 2019. *Phegopteris excelsior* (Thelypteridaceae): A new species of North American tetraploid beech fern. Novon 27:211–218.

Pederson G. T., L. J. Graumlich, D. R. Fagre, T. Kipfer, and C. C. Muhlfeld. 2010. A century of climate and ecosystem change in Western Montana: what do temperature trends portend? Climate Change 98:133–154.

Ponce, M. M. and M. A. Scataglini. 2018. Further progress towards the delimitation of *Cheilanthes* (Cheilanthoideae, Pteridaceae), with emphasis on South American species. Organisms Diversity and Evolution 18:175–186.

Popovich, S. and D. R. Farrar. 2020. *Botrychium furculatum* (Ophioglossaceae), a new moonwort species from the Rocky Mountains of North America. American Fern Journal 110:165–182.

PPG 1 (Pteridophyte Phylogeny Group). 2016. A community-derived classification for extant lycophytes and ferns. Journal of Systematics and Evolution 54:563–603.

Pryer, K. M. and C. H. Haufler. 1993. Isozymic and chromosomal evidence for the allotetraploid origin of *Gymnocarpium dryopteris* (Dryopteridaceae). Systematic Botany 18:150–172.

Resler, L. M. and D. F. Tomback. 2008. Blister rust prevalence in krummholz whitebark pine: implications for treeline dynamics, northern Rocky Mountains, Montana, USA. Arctic, Antarctic, and Alpine Research 40:161–170.

Rothfels, C. J., M. A. Sundue, L.-Y. Kuo, A. Larsson, M. Kato, E. Schuettpelz, and K. M. Pryer. 2012. A revised family-level classification for eupolypod II ferns (Polypodiidae: Polypodiales). Taxon 61:515– 533.

Rothfels, C. J., M. D. Windham, and K. M. Pryer. 2013. A plastid phylogeny of the cosmopolitan fern family Cystopteridaceae (Polypodiopsida). Systematic Botany 38:295–306.

Rothfels, C. J., A. K. Johnson, M. D. Windham, and K. M. Pryer. 2014. Low-copy nuclear data confirm rampant allopolyploidy in the Cystopteridaceae (Polypodiales). Taxon 63:1026–1036.

Schneller, J. J. 1989. Remarks on hereditary regulation of spore wall patterns in intra- and interspecific crosses of *Athyrium*. Botanical Journal of the Linnean Society 99:115–123.

Sessa, E. B., E. A. Zimmer, and T. J. Givnish. 2012. Unraveling reticulate evolution in North American *Dryopteris* (Dryopteridaceae). BMC Evolutionary Biology 12:104.

Shackleford, I. 1997. *Evolutionary and systematic studies of* Isoëtes *in western North America*. Ph.D. dissertation, Miami University, Ohio.

Shmakov, A. I. 2015. A new system of family Woodsiaceae. Turczaninowia 18:11–16.

Sigel, E. M., M. D. Windham, and K. M. Pryer. 2014. Evidence for reciprocal origins in *Polypodium hesperium* (Polypodiaceae): A natural fern model system for investigating how multiple origins shape allopolyploid genomes. American Journal of Botany 101:1476–1485.

Smith, A. R., K. M. Pryer, E. Schuettpelz, P. Korall, H. Schneider, and P. G. Wolf. 2006. A classification for extant ferns. Taxon 55:705–731.

Soltis, P. S. 2017. Digitization of herbaria enables novel research. American Journal of Botany 104:1281–1284.

Standley, P. C. 1920. Ferns of Glacier National Park, Montana. American Fern Journal 10:97–110.

Standley, P. C. 1921. Flora of Glacier National Park, Montana. Contributions to the U.S. National Herbarium 22:235–438.

Steere, W. C. 1945. Robert Statham Williams (1859-1945). The Bryologist 48:93–99.

Stensvold, M. C. and D. R. Farrar. 2016. Genetic diversity in the worldwide *Botrychium lunaria* (Ophioglossaceae) complex, with new species and new combinations. Brittonia 69:148–175.

Testo, W., A. Haines, and A. V. Gilman. 2016. *Huperzia continentalis* (Lycopodiaceae), a new species of gemmiferous firmoss separated from *Huperzia haleakalae*. Systematic Botany 41:894–900.

Thomas, I. and J. Mow. 2016. Waterton-Glacier International Peace Park. Waterton-Glacier International Peace Park. http://naturalresourcespolicy.org/docs/Hands%20Across%20Borders/TBC%20Profiles/TBC%20Profile_Waterton%20Glacier%20International%20Peace%20Park_Freimund.pdf Retrieved 3 January 2021.

Thomson, J. A., J. T. Mickel, and K. Mehltreter. 2008. Taxonomic status and relationships of bracken ferns (*Pteridium*: Dennstaedtiaceae) of Laurasian affinity in Central and North America. Botanical Journal of the Linnean Society 157:1–17.

Tryon, R. M. 1955. *Selaginella rupestris* and its allies. Annals of the Missouri Botanical Garden 42:1–99.

United States Geological Service. 2020. Repeat Photography Project. https://www.nps.gov/glac/learn/nature/glacier-repeat-photos.htm Retrieved 3 January 2021.

Wagner, W. H. Jr. and L. P. Lord. 1956. The morphological and cytological distinctness of *Botrychium minganense* and *B. lunaria* in Michigan. Bulletin of the Torrey Botanical Club 83:261–279.

Wagner, W. H., Jr., F. S. Wagner, C. H. Haufler, and J. K. Emerson. 1984. A new nothospecies of moonwort (Ophioglossaceae, *Botrychium*). Canadian Journal of Botany 62:629–634.

Wagner, W. H. and J. M. Beitel. 1993. Lycopodiaceae. Pp. 18–37, *in* Flora of North America Editorial Committee (eds), *Flora of North America North of Mexico. Volume 2. Pteridophytes and Gymnosperms*. Oxford University Press, New York.

Wagner, W. H., Jr. and F. S. Wagner. 1993. *Botrychium*. Pp. 86-101, *in* Flora of North America Editorial Committee (eds), *Flora of North America North of Mexico. Volume 2. Pteridophytes and Gymnosperms*. Oxford University Press, New York.

Wagner, W. H., Jr., R. C. Moran, and C. R. Werth. 1993. Aspleniaceae. Pp. 228–245, *in* Flora of North America Editorial Committee (eds.), *Flora of North America North of Mexico. Volume 2. Pteridophytes and Gymnosperms*. Oxford University Press, New York, NY.

Wagner, W. H. Jr. and J. R. Grant. 2002. *Botrychium alaskense*, a new moonwort from the interior of Alaska. American Fern Journal 92:164–170.

Wei, R., A. Ebihara, Y.-M. Zhu, C.-F. Zhao, S. Hennequin, and X.-C. Zhang. 2018. A total evidence phylogeny of the lady fern genus *Athyrium* Roth (Athyriaceae) with a new infrageneric classification. Molecular Phylogenetics and Evolution 119:25–36.

Windham, M. D. 1993a. New taxa and nomenclatural changes in the North American fern flora. Contributions from the University of Michigan Herbarium 19:31–61.

Windham, M. D. 1993b. *Woodsia*. Pp. 270–280, *in* Flora of North America Editorial Committee (eds), *Flora of North America North of Mexico. Volume 2. Pteridophytes and Gymnosperms*. Oxford University Press, New York.

Xu, K.-W., L. Zhang, C. J. Rothfels, A. R. Smith, R. Viane, D. Lorence, K. R. Wood, C.-W. Chen, R. Knapp, L. Zhou, N. T. Lu, X.-M. Zhou, H.-J. Wei, Q. Fan, S.-F. Chen, D. Cicuzza, X.-F. Goa, W.-B. Liao, and L.-B. Zhang. 2020. A global plastid phylogeny of the fern genus *Asplenium* (Aspleniaceae). Cladistics 36:22–71.

Zhang, L., X.-P. Fan, S. Petchsri, L. Zhou, R. Pollawatn, X. Zhang, X.-M. Zhou, N. T. Lu, R. Knapp, S. Chantanaorrapint, P. Limpanasittichai, H. Sun, X.-F. Gao, and L.-B. Zhang. 2020. Evolutionary relationships of the ancient fern lineage the adder's tongues (Ophioglossaceae) with description of *Sahashia* gen. nov. Cladistics 36:380–393.

Zika, P. F. and D. R. Farrar. 2009. *Botrychium ascendens* W. H. Wagner (Ophioglossaceae) in Newfoundland and notes on its origin. American Fern Journal 99:249–259.

Acknowledgements

We are most grateful to staff members at Glacier National Park, especially Dawn Lafleur, Rebecca Lawrence, Jen Asebrook, Jen Guse, and Jean Tabbert (who manages the Herbarium), for their generous help and support with facilitating KH's fieldwork in summer 2019. This paper is part of a master's thesis in Education completed at Duke University in 2019 by KH, under the guidance of KMP and MDW. KH acknowledges support from Naomi Kraut (Director of Master of Arts in Teaching Program at Duke), a Durham Teaching Fellowship, and the Robert Noyce Fellowship for providing this opportunity for independent study. We also thank Daniel F. Brunton (Ottawa, Canada) for his helpful insights on the status of *Isoëtes* in Glacier National Park. In addition, we appreciate input from Edward R. Alverson on the taxonomy of *Athyrium*, as well as confirming some of our photos posted to iNaturalist. We particularly wish to acknowledge how important the NSF-funded Integrated Digitized Biocollections (iDigBio) resources were to this project by making herbarium specimen data and high-resolution images available on online portals. The following herbaria were most generous during the 2020-21 pandemic in arranging either the shipment of herbarium loans, or the delivery of high-resolution images that were otherwise unavailable, for our examination: GH, MONT, MONTU, SAT, SRP, UTC, WTU. We thank the Associate Editor, Dr. Susan Fawcett, as well as Dr. John Game and an anonymous reviewer for their thoughtful comments and suggestions.

American Fern Journal 111(4):251–307 (2021)
Published on 5 November 2021

The Scaly Tree Ferns Allied to *Cyathea multiflora* (Cyatheaceae) in Colombia and Neighboring Countries

Marcus Lehnert*
Herbarium (HAL), Martin-Luther-Universität Halle Wittenberg, Neuwerk 21, 06108 Halle (Saale), Germany. email: marcus.lehnert@botanik.uni-halle.de
Nees-Institut für Biodiversität der Pflanzen, Rheinische Friedrich-Wilhelms Universität, Meckenheimer Allee 170, D-53115 Bonn, Germany.

Adrian tejedor
Wildlife Conservation Society – Papua New Guinea, Rohanoka St., Goroka, Papua New Guinea. email: adriantejedor@gmail.com

Wilson D. Rodríguez Duque
Instituto Amazónico de Investigaciones Científicas -Sinchi, Calle 20 No. 5-44, Bogotá, Cundinamarca, Colombia. email: wdropteris@hotmail.com

Luis Fernando Giraldo Gallego
Universidad CES, Calle 10 A No. 22 - 04, Medellín, Antioquia, Colombia
Herbario Universidad de Antioquia (HUA), Calle 67 Número 53-108, Medellín, Antioquia, Colombia. email: ferngiraldo@yahoo.com

Abstract.—We present an update to our knowledge of the taxonomically challenging *Cyathea multiflora*-group. Several taxa can be reinstated and newly described thanks to extensive field studies in Colombia and bordering countries. Easily overlooked characters like minute hairs, laminar squamules, and size of indusia correlate with distinct physiognomies in the field. *Cyathea multiflora* in the strict sense is almost restricted to Mesoamerica, just reaching into the Colombian Darién region. We observe a geographic overlap of several species especially in the Darién-Chocó region (*Cyathea hildegardis sp. nov., C. pinnula, C. pinnuloides sp. nov., C. retanae*) and two wider-ranging species extending from Mesoamerica into the Andes (*C. acutidens, C. pinnula*). The reinstated *C. columbiana* and newly recognized *C. uregoana sp. nov.* and *C. prosopioides sp. nov.* are restricted to the Chocó, including the Ecuadorean Esmeraldas region. Frequently found in the northern Colombian Cordillera central is *C. paisa sp. nov.*, which is intermediate between *C. pinnuloides* of the Darién-Chocó region and *C. lindigii*, a relatively large species widespread in the Cordillera Oriental and the eastern Andean slopes south to Bolivia. We retain *C. acutidens* and *C. leucolepismata* as distinct species that can also be readily distinguished in the field by their appearance and the shape of the entire leaves but can be difficult to differentiate as fragmentary specimens. *Cyathea mariposana sp. nov.*, a trunkless species presumably more closely related to *C. squamulosa*, is described from Panama. *Cyathea retanae* is reported from Colombia. A lectotype is chosen for *C. columbiana*. All relevant species are illustrated and incorporated in a diagnostic key.

Key Words.—Biogeography; Costa Rica; lectotype; Mesoamerica; Panama

Cyathea multiflora Sm. is a neotropical scaly tree fern (Cyatheaceae) with a long confusing taxonomic history. It is one of the few tree fern species described in the 18th century (Smith, 1793), and, as is the nature of such old names, the type material is fragmentary and not well documented. Its

* author for correspondence

provenance was once dubious because despite being annotated as "Amer. Merid.", it was first published as being from Jamaica, until Maxon (1912) ruled out this possibility. In his revision of the genus *Cyathea*, Tryon (1976) cites eight basionyms as synonyms under *C. multiflora*, stating that "the variation in [. . .] several characters shows some correlation with geography, and with each other. However, they are weak and do not provide a basis for the recognition of other taxa." This statement certainly stems from the relative paucity of field observations made and documented in past times. Once botanists took the opportunity to study these plants repeatedly in the field, differences emerged between these synonymized taxa. Rojas-Alvarado (2001) was able to convincingly reinstate *Cyathea acutidens* Christ and *C. squarrosa* (Rosenst.) Domin, and to further recognize *C. grayumii* A.Rojas and *C. rojasiana* Lehnert (as *C. panamensis* A.Rojas, *nom. illeg.*) as new to science based on observations made in Costa Rica and Panama. But just increased sample size can also help in distinguishing more taxa. In his floral studies for Mesoamerica and Ecuador, based on ample collections specifically gathered for this purpose, Moran (1991, 1995) was able to differentiate several taxa from *C. multiflora sensu lato*, sometimes describing them first as new species, that had been treated as synonyms, dubious names, or putative hybrids by Tryon (1976), *i.e. C. squamulosa* I.Losch, *C. pinnula* (Christ) Domin, *C. holdridgeana* Nisman & L.D.Gómez (as *Cyathea albomarginata* R.C.Moran) and *C. leucolepismata* Alston (as *C. amazonica* R.C.Moran). As field explorations advanced, even more names were revalidated (*C. austroamericana* Domin, *C. lindigii* (Baker) Domin; Lehnert, 2011). The types of the few remaining synonyms of *C. multiflora* come from less accessible areas in Panama and Colombia. We assumed that some may represent further distinct morphotaxa, and indeed we were able to identify several more during our latest forays in these countries. In the following we report the results of our comparative taxonomic studies, aiming on one hand to resolve this taxon group for Colombia, and on the other hand to clarify the circumscription of *C. multiflora* proper.

Materials & Methods

This study makes use of data gathered from the largest Colombian herbaria (CAUP, COAH, COL, CUCV, FMB, HUA, JAUM, MEDEL, TULV, VALLE; Thiers, 2019). Other collections were consulted for types and comparative material either on loan or during visits to AAU, B, BM, F, GOET, HAL, K, L, M, MO, P, STU, UC, US, W and Z. Field trips led the authors to all ecoregions of Colombia (FG & WR 2000–2016, & ML, 2015; FG & AT 2015) and Panama (AT & ML, 2016). Specimens of the authors' collections are mainly deposited at HUA, COAH, and PMA, with further duplicates deposited at BONN and Z. Terminology follows Lellinger (2002) and Lehnert (2011). We focus only on material that after Tryon (1976) would key out as *C. multiflora*, thus excluding from his "Group of *Cyathea multiflora*" the South American *C. andina* (H.Karst.) Domin, *C. platylepis* (Hook.) Domin and *C. vilhelmii* R.M.Tryon, the Caribbean *C. parvula* (Jenman) Domin, and the eastern Pacific island endemics *C.*

weatherbyana (C.V.Morton) C.V.Morton (Galapagos Islands), *C. alfonsiana* L.D.Gómez, and *C. notabilis* Domin (both Cocos Island). These taxa had been already set apart from *C. multiflora* based on morphology (Lehnert, 2011), and, with the exception of *C. notabilis,* were confirmed as being not closely related to it in molecular studies (Kao *et al.,* 2015; Loiseau *et al.*, 2019, Lehnert *et al.*, unpublished data).

Results & discussion

We recognized several species as new to science (*Cyathea hildegardis sp. nov., C. mariposana sp. nov., C. paisa sp. nov., C. pinnuloides sp. nov., C. prosopioides sp. nov., C. uregoana sp. nov.*) or as newly reinstated (*C. columbiana* Domin) from the synonymy of *Cyathea multiflora sensu* Tryon (1976). Most of these novelties are found in the Chocó region of western Colombia (Pérez-Escobar *et al.*, 2019).

The species of this group have distinct character combinations composed from habit (*i.e.,* trunkless plants to trunks several meters tall, leaves stiffly erect to arching), number of pinna pairs per frond, pinnule tip shape (rounded to caudate), laminar indument (*e.g.,* hairs present/absent, only on veins or also between them, small scales absent or present, flat or also bullate, strongly vs. weakly bullate), and indusium size (*i.e.,* reaching more than one quarter around the receptacles vs. less than that). Petiole scale color ranges from strongly bicolorous dark brown with white margins (these often transient with almost completely white scales, *e.g., C. leucolepismata*) to concolorous orange (*e.g., C. paisa*) and dark red brown to blackish with paler margins (*e.g., C. hildegardis*). However, the petiole scales in about half of the species in this group vary between bicolorous and concolorous in one individual (*e.g., C. columbiana, C. multiflora, C. pinnuloides*). With few exceptions, absolute maximum sizes of pinnae and pinnules are quite reliable, species-specific features in this group (Fig. 1). For each species, we usually allow for the occurrence of both depauperate and luxurious plants, and the initial amplitude of size in the *Cyathea multiflora* aggregate (*sensu* Tryon 1976) was, though large, also very gradual between the extremes. Yet, in combination with other morphological characters, size works well for delimiting the species of the *C. multiflora* group (Fig. 1).

The morphological taxa thusly circumscribed further align with geographical units, as we see several taxa centered either in northern Mesoamerica (*C. austroamericana, C. grayumii*), southern Mesoamerica + Chocó (*C. acutidens, C. mariposa, C. multiflora, C. pinnula, C. retanae, C. rojasiana*), northern Andes (*C. hildegardis, C. paisa, C. pinnuloides*), and eastern Andean cordillera + Amazonia (*C. leucolepismata, C. lindigii*) (Fig. 2).

We could not verify an occurrence of this group in Venezuela; in fact, it seems to be absent already in eastern Colombia, from the Sierra Nevada de Santa Marta and most of the Cordillera Occidental NE of Bogota. Venezuelan and Guayanan material determined as *C. multiflora* belongs to other species,

FIG. 1. Morphological overview of the *Cyathea multiflora* aggregate. All pinnae are shown at the same scale and represent the largest ones preserved in the specimens. Species on the left are mainly from Mesoamerica, species on the right are from South America. A. *Cyathea acutidens* (*M. Lehnert 3026*, HAL); B. *Cyathea austroamericana* (*Cafferty et al. 81A*, MO). C. *Cyathea columbiana* (*M. Lehnert 1582*, GOET); D. *Cyathea leucolepismata* (*Ewan 16784*, isotype COL); E. *Cyathea lindigii* (*A. Lindig 310*, isotype P); F-G. *Cyathea multiflora:* F. (*R. Shakespeare s.n.*, holotype BM), G. (*M. Lehnert 3497 with A. Tejedor*, BONN); H. *Cyathea paisa* (*M. Lehnert 3022*, paratype BONN); J. *Cyathea pinnula* (*M. Lehnert 3503*, BONN); K. *Cyathea prosopioides* (*J.L. Fernández Alonso et al. 9143*, holotype COL); L. *Cyathea uregoana* (*D.B. Lellinger & E.R. de la Sota 892*, holotype COL). Not shown for technical reasons are *C. hildegardis* (most similar to C) and *C. pinnuloides* (intermediate between K and C).

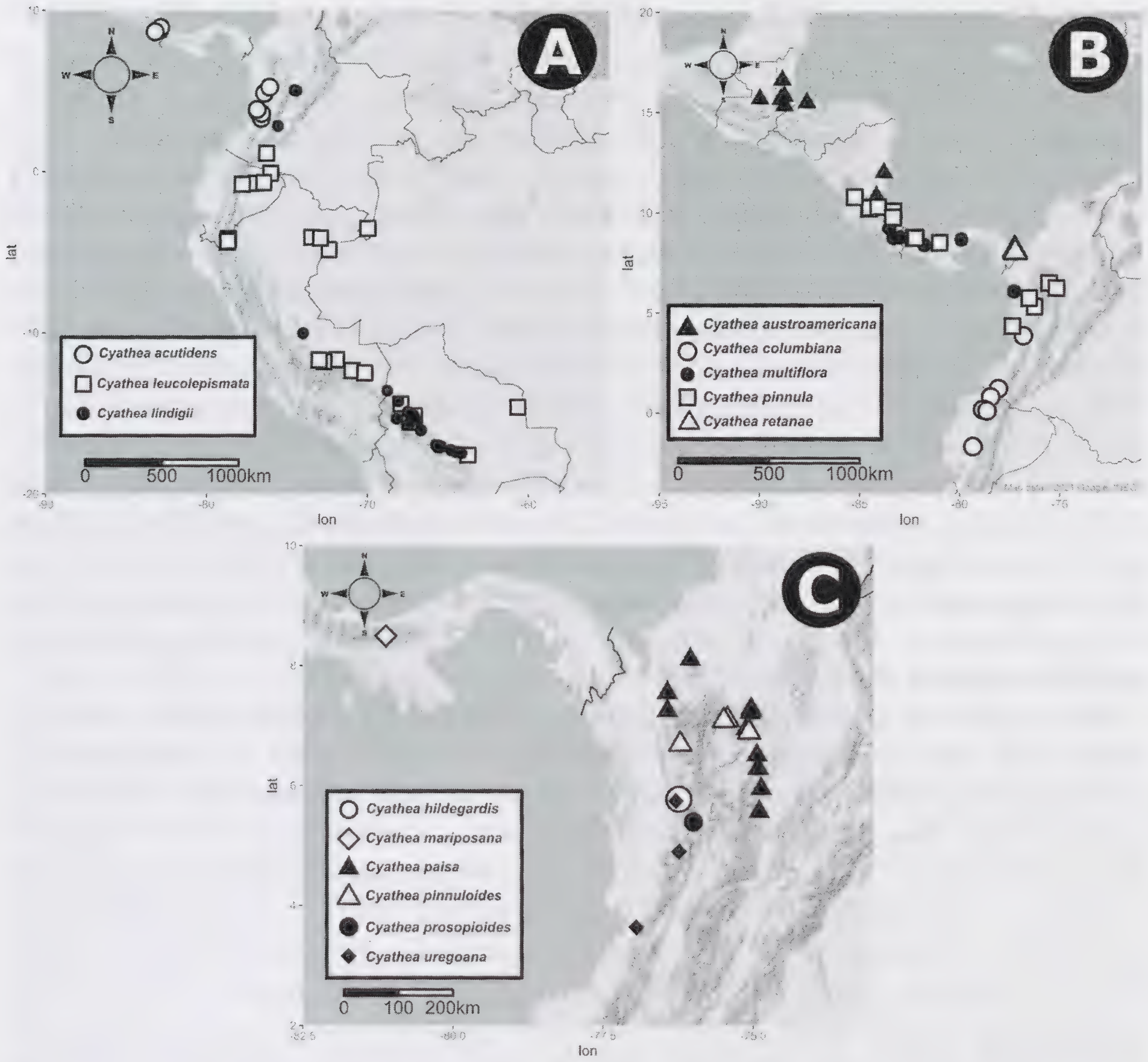

FIG. 2. Geographical overview of the *Cyathea multiflora* aggregate. A: *C. acutidens* (circles); *C. leucolepismata* (squares); *C. lindigii* (dots). B: *C. austroamericana* (black triangles); *C. columbiana* (circles); *C. multiflora* (dots); *C. pinnula* (squares); *C. retanae* (white triangles). C: *C. hildegardis* (circle); *C. mariposana* (white diamond); *C. paisa* (black triangle); *C. pinnuloides* (white triangle); *C. prosopioides* (dot); *C. uregoana* (black diamond).

mostly *Cyathea andina* and *C. cyatheoides* (Desv.) K.U.Kramer (Lehnert, 2011).

Despite our efforts, we could not satisfactorily resolve two species complexes because their center of distribution lies outside of our geographic focus of Colombia. Getting sufficient comparative material through additional loans was deemed unfeasible at this point, especially as herbarium specimens do not provide important characters that we learned to appreciate during this study.

One of these complexes is *C. multiflora* itself. The type of this name and the synonym next in line, *C. denticulata*, both lack petiole material, and the first has only a vague, the other a dubious provenance. Both type collections are

parts of relatively small leaves with blunt-tipped pinnules, very much as *C. austroamericana* (Fig. 1), a similar species with a parapatric distribution in northern Mesoamerica (Fig. 2B), and also formerly synonymized under *C. multiflora sensu lato* (Tryon, 1976). The type of *C. austroamericana* (= *Hemitelia nigricans* C.Presl. [*E. von Friedrichsthal s.n.*; W-0052584, W-0052585]) also lacks petiole material; the locus classicus is given as "Guatemala, ad ripas fl. St. Juan, 1841". Some authors seem to have interpreted this locality as the Río San Juan valley in Nicaragua (Tryon, 1976); von Friedrichsthal demonstrably has travelled and collected here, shortly after the breakup of the República Federal de Centroamérica (1823–1840), which span from Guatemala to Costa Rica (Soria, 1987). A labeling error or confusion may have occurred, but von Friedrichsthal indeed also collected in Guatemala, where a lesser known Río San Juan exists. The specimen *Cafferty et al. 81A* (MO) from Belize matches the type of *C. austroamericana* in laminar characters well (except that the pinnules are here mostly acute and not blunt) and has blackish petiole scales with white margins (Lehnert, 2011). Our concept of *C. austroamericana* having a different, darker petiole scale colour than *C. multiflora* stems from this alignment.

The presence of plants with more orange-brown petiole scale margins, which we would address as *C. multiflora,* in Guatemala is confirmed by photographs (Véliz Pérez and Vargas Ponce, 2006), but association of these plants with the type of *C. multiflora* (or *C. denticulata*, and not *C. austroamericana*) is purely conjectural and serves nomenclatural stability by adhering to established concepts (Rojas-Alvarado, 2001; Lehnert, 2011). The few confirmed plants of *C. multiflora* from northern Mesoamerica have blunt-tipped pinnules, while from Costa Rica to the Darién region of Colombia, plants have mostly acute to short attenuate pinnule tips (Fig. 1) and tend to have more and more laminar hairs as one goes east (the hairy extreme representing the type of the synonym *C. hartii* from Panamá). Further extensive field work may elucidate how many occurrences of *C. multiflora* are hidden among the records of *C. austroamericana* reported here (Fig. 2B).

The other unresolved complex is that of *Cyathea leucolepismata,* a taxon here considered to be restricted to the Amazon basin (Fig. 2A). It has been considered synonymous with *C. acutidens* by Rojas-Alvarado (2007), and some individuals seem to bridge the morphological gap separating the two taxa. Specifically, the petiole scales of *C. leucolepismata* seem to have a high variability of color, which are mostly whitish to pale brown, but occasionally almost completely dark brown blackish with whitish margins on the trunks and the lower petioles. It is assumed here that a separate population of *C. leucolepismata* with such aberrant, mostly dark brown petiole scales forms the basis for reports of *C. andina* (H.Karst.) Domin from the Guyana shield and *C. lindigii* from the central Andes, but this requires further study. This is another example of how one otherwise reliable distinguishing character can go awry in one particular species complex. Species of the *C. multiflora* aggregate are also unreliable in some leaf characters.

The shape of the lamina apex has been used in tree fern taxonomy since the revision of *Cnemidaria* by Stolze (1974), who defined the term "gradually reduced" and "abruptly reduced" as well as "conform" and "non-conform apical section" as subclasses of the abruptly reduced apex. A conform apical section is shaped like a lateral pinna and is the more easily understood form of the abruptly reduced lamina. Some species have only conform apical sections, like *C. impar* R.M. Tryon and *C. bipinnata* R.C. Moran (Lehnert and Weigand, 2017). However, abruptly reduced apices are not necessarily pinna-like, *i.e.*, conform. A non-conform apical section is not shaped like a lateral pinna but is more triangular, tapering in itself and thus hardly distinguishable from a gradually reduced laminar apex in herbarium specimens. In the whole leaf, however, a non-conform apical section clearly stands apart from the rest of the lamina; but it can also be just one extreme condition in some variable species, *e.g.*, *C. multiflora* varying between conform and non-conform apices, and *C. uregoana* between non-conform and gradual apices. Photographs or at least scrutinous field notes are necessary to allow a secure characterization of the plants for taxonomic studies.

Most studied specimens of the *Cyathea multiflora* alliance present on their laminae the same black acicular fungal fruiting bodies described for *Cyathea pinnula* (Moran 1991). The fungi seem to be associated with hairs and trichomidia and are thus more frequently observed in the hairy species like *C. leucolepismata, C. pinnula, C. pinnuloides, C. hildegardis,* and *C. uregoana* and less in the glabrescent species like *C. multiflora, C. austroamericana,* and *C. lindigii.*

Taxonomic Treatment

1. *Cyathea acutidens* (Christ) Domin, Pteridophyta 264: 1929. *Alsophila acutidens* Christ, Bull. Herb. Boissier II. 6: 186. 1906. *Alsophila leucolepis* Mart. var. *pubescens* Christ in Pittier, Prim. Fl. Costaric. 3: 42. 1901. Type.—COSTA RICA. Puntarenas: Cañas Gordas, [ca. 8.75, -82.9166667] 1100 m, Feb 1897, *H. Pittier 10992* (lectotype: P-00625698!, chosen by Lehnert, 2011:49; isolectotypes: NY-148820! [fragment], P-00625697 [Herb. Bonaparte; image!], US-01448382 [image!]/-01448391 [image!]). Remaining syntypes (lectoparatypes): Same locality, same date, *H. Pittier 10981* (BR-0000006977801 [image!]/-0000006978709 [image!]/-0000006978792 [image!], NY-148819! [fragment], P?, UC-1550953!, US-00066091 [image!]/-01100701 [image!]), *H. Pittier 10989* (BR-0000006978730 [image!], NY-148818! [fragment], P-00625696 [Herb. Bonaparte; image!], US-01448383 [image!]). **Fig. 3A–C.**

Trunks to 3.5 m tall, 10–14 cm diam.; trunk covered with often prickly old petiole bases; apices hidden between petiole bases; without adventitious buds. Leaves to 320 cm long, unfolding only one at a time; dead leaves sometimes forming a skirt below the crown. Petioles 15–75 cm long, inermous to scatteredly aculeate with prickles to 3 mm long, pale brown to dark brown, stramineous or ochre, matte, glabrescent with scattered to dense scurf

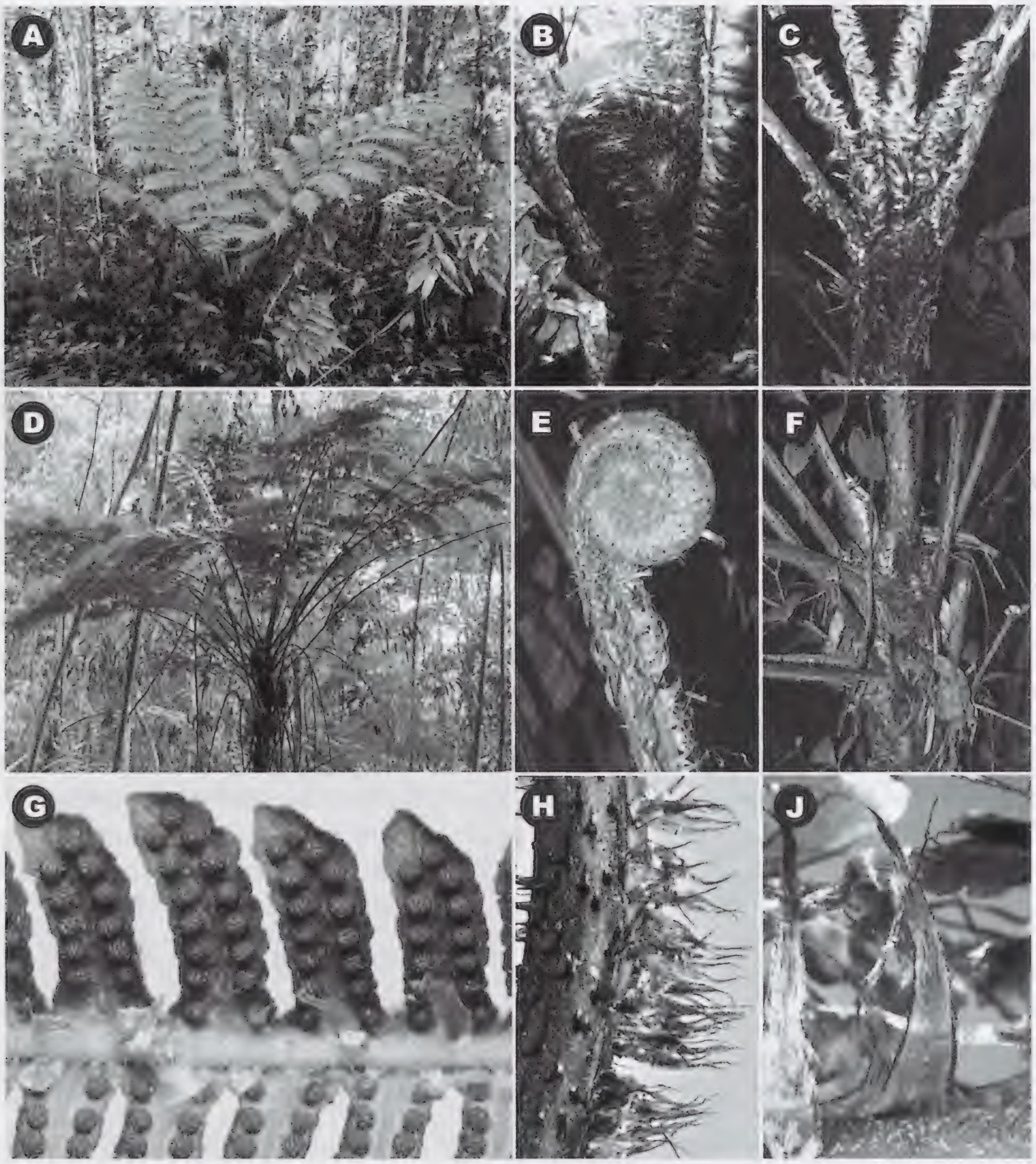

FIG. 3. Field characters. A–C. *Cyathea acutidens* (Valle del Cauca, Colombia; photos M. Lehnert): A. Habit. B. Petiole and crozier with scales. C. Trunk apex. D–J. *Cyathea leucolepismata*: D. habit (Napo, Ecuador; photo A. Tejedor). E. Petiole and crozier with scales. F. Trunk apex (Zamora-Chinchipe, Ecuador; photo M. Lehnert): G: Fertile segments, showing laminar hairs and scales (Caquetá, Colombia; photo F. Giraldo). H. Detail of aculeate petiole, with darker scales (Caquetá, Colombia; photo F. Giraldo). J. Detail of darker scale with characteristic marginal teeth and blurred central streak (Caquetá, Colombia; photo F. Giraldo).

consisting of tan to white hairs 0.5–0.8 mm long, and arching to appressed, unicellular trichomidia, without squamules; petioles basally with a discontinuous line of pneumathodes to 9 × 1 mm on each side, dark brown and inconspicuous in dried material. *Petiole scales* ovate-lanceolate to lanceolate,

to (12.0–)17.0–26.0 × (3.5–)4.0–6.0 mm, mostly discordantly bicolorous to almost concolorous, pale brown to ochre with lighter brown to whitish margins, sometimes centers partly dark brown; differentiated margins without setae or teeth, fragile, usually abraded. *Laminae* 90–270 × 80–150 cm, bipinnate-pinnatifid, obovate-elliptic, firm herbaceous, matte dark-green adaxially, gray-green abaxially; basally tapering, apices gradually reduced. *Rachises* inermous to sparsely muricate proximally, dark stramineous to pale brown abaxially and adaxially; with scattered to dense white to tan, curved multicellular hairs to 0.5–0.8 mm long adaxially, abaxially glabrescent with scurf like that on the petioles, mainly flaccid hairs. *Pinnae* to 75 cm long, sessile to stalked by 1.0 cm, (12–)16–18 pairs, weakly ascending, alternate, inarticulate, distally narrowly to broadly green-alate, distal segments simply adnate before ending in a pinnatifid apical section; basal pairs much smaller than the medial pinnae, notably reflexed. *Costae* to 1.5–2.5 mm wide, inermous to sparsely verrucate, dark orange–brown to grayish brown abaxially, ochre to dark stramineous adaxially; adaxially with many tan to brown multicellular hairs, curved, to 0.8(–1.0) mm long, abaxially with very thin appressed hairs and brown scurf similar to the scurf on the rachises; junctures of costae and rachises weakly swollen abaxially, often black when dried, bearing each a planar elliptic pneumathode to 3.0–3.5 × 1.0–1.5 mm, orange-brown, conspicuous. Largest *pinnules* 90–100 × 20–22 mm, sessile, inarticulate, 1.5–2.0 cm between the stalks/costules, linear-oblong, truncate basally, long-acuminate to short-attenuate apically with serrate to crenulate margins; *costules* yellowish brown to stramineous adaxially and abaxially, proximally often darker brown, strongly prominent, ridged, and densely hairy adaxially with tan to brown, curved multicellular hairs to 0.5(–1.0) mm long, abaxially weakly prominent, densely hairy with erect, white, thin multicellular hairs, also with some white to basally tan squamules, bullate ones to 0.8–1.0 mm long, flat lanceolate ones to 3 × 1 mm, with entire margins and short-attenuate tips; costules basally without pneumathodes, but often with a black spot abaxially in dried specimen. *Segments* to 12.0 × 4.0–5.0 mm, sessile, adnate, never remote, patent to weakly ascending, distally falcate, tips obtuse to rounded; proximal segments alternate to subopposite, usually as long as following segments; sinuses acute, to 0.5–1.0 mm wide; margins deeply crenate-dentate to serrate; margins not differently incised in proximal segments of a pinnule; veins planar on both sides or weakly protruding adaxially, brown; veins adaxially with some multicellular hairs to 0.5 mm long, abaxially hairy with many erect to curved, white multicellular hairs to 0.5–0.8 mm long, also scattered between the veins; sterile veins simple or forked, fertile veins forked. *Sori* 0.6–0.8(–1.0) mm diam., medial to supramedial, appearing submarginal if lobes of segments are revolute, in the fork of veins, immature pale whitish-yellow, mature dark orange-brown; indusia hemitelioid, reaching 1/4 to 1/3 around the receptacles, glabrous, yellowish brown to white, matte, firm, margins with shallow lobes, appressed to ascending but not arching over sori, completely covered by intact sori; indusia usually preserved in over-mature sori; receptacles globose, 0.3(–0.4) mm

diam., paraphyses numerous, flaccid, hyaline, white to tan, much longer than the sporangia (0.5–0.6 mm long). Spores not examined.

ETYMOLOGY.—The name refers to the sharply serrate segment margins (Christ, 1906).

DISTRIBUTION AND HABITAT.—Costa Rica and Colombia (Fig. 1) at 1100–1800 m, to be expected from western Panamá because the type locality is located at the border to Costa Rica; photographic records also from northern Ecuador.

ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. **Puntarenas:** Trail N of gravel pit just NE of Las Alturas between Río Bellavista and Fila Cedro, 1600–1800 m, 16 Feb 1991, *F. Almeda, T.F. Daniel & B. Bartholomew 6661* (UC); Fila El Tigre, SE of Las Alturas 08°56′N, 82°51′W, 1350–1450 m, 29 Aug 1983, *G. Davidse 24107* (MO, UC); 6 km S of San Vito de Java, [ca. 08°47′37"N, 82°57′18″W] 1220 m, 1973, *B. McAlpin 2306* (F); vicinity of Biological Field Station at Finca Wilson, 5 km S of San Vito de Java, [ca. 08°47′37"N, 82°57′18″W] 1100–1200 m, 02–04 Aug 1967, *J.T. Mickel 3187* (UC); at Finca Wilson, 5 km S of San Vito de Java, [ca. 08°47′37″N, 82°57′18″W] 1100–1200 m, *R.G. Wilson. & C. Wilson 69-24* (UC).

COLOMBIA. **Cauca:** El Tambo, El Tambo – PNN Munchique, between Uribe and "La 81" (La Romelia), 3.5344833, -76.6022472, 1800 m, 12 Apr 2015, *M. Lehnert 3126 with M. Kessler, F. Giraldo, W.D. Rodríguez* (BONN, HUA, Z). **Valle del Cauca:** Cali, Vereda Villa Carmelo, 3.7500000, -76.8333333, 1700 m, 15 May 1982, *H. Murphy 396* (TULV); La Cumbre, Finca Kyburz, ladera oriental sobre el río Bitaco, valle de Bitaco, 1 kilómetro sobre y al oriente de Bitaco, 3.3048833, -76.6020806, 1300 m, *P. Hutchinson 3144* (COL); Yotoco, vía Buga - Buenaventura, km 18, 3.6108333, -76.5908333, 1600 m, 8 Oct 1978, *C. Barbosa 648* (FMB); Buga, región del Calima Vía vía Buenaventura, Bosque de la Facultad, 4.8666667, -76.4000000, 1400 m, 25 May 1967, *H. García-Barriga 18822* (COL); Yotoco, Reserva Yotoco, 3.8586111, -76.8588889, 1600 m, 8 Feb 2015, *M. Lehnert 3088* (BONN, HUA, Z); Dagua, above Loboguerrero, km 23 along road to Cali, 5.2416667, -76.0822222, 1550 m, 11 Mar 2015, *M. Lehnert 3112* (BONN, HUA, Z).

The description of *Alsophila acutidens*, though being more elaborate than the description of *A. leucolepis* Mart. var. *pubescens*, represents only a *stat. nov.* and *nom. nov.* based on the earlier published varietal name. The varietal epithet is blocked at species rank by *Alsophila pubescens* Baker (Hooker and Baker, 1868) and *Cyathea pubescens* Kuhn (1869).

Christ (1906) designated as type of *Alsophila acutidens* the material in his herbarium, today integrated in P. Three collection numbers are cited, but the first two are identical (*i.e., 10891, 10891, 10992*), which is interpreted as a type setting error because *H. Pittier 10981, 10989* and *10992* had been cited in the earlier description of *A. leucolepis* var. *pubescens* (Christ in Pittier 1901). We could also find true material of this species with congruent label information under the numbers *H. Pittier 10981, 10989* and *10992*, of which multiple duplicates exist in several herbaria. When choosing a lectotype, it would be

most unambiguous to simply take the first mentioned number *10981* over the following *10989* and *10992*. Each is supposedly present in P (https://plants.jstor.org), but *H. Pittier 10981* (P-00634035/-00634036) is in fact not this Costa Rican tree fern specimen (as the material at BR, UC, and US) but a Boraginaceae annotated as the type of *Cordia volubilis* Pittier (Pittier, 1929), collected 25 years later in Venezuela. Of the available material at P that represents this tree fern species, most come from the Herb. Bonaparte, and only P-006256898 (*H. Pittier 10992*), besides lacking any additional herbarium assignment, has the original printed label provided by Pittier filled out by a different handwriting, which matches that from the labels of the Herb. Christ. This specimen is also the only one where "*Alsophila acutidens n. sp.* [det.] Christ" is annotated. In conclusion, *H. Pittier 10992* (P-006256898) was the prime choice for lectotype (Lehnert, 2011).

All Pittier collections from Costa Rica that form the type material represent large plants of the same species, with clearly serrated segment margins. Unfortunately, petiole scales are not preserved in any of them. Our picture of the Costa Rican population is complemented by additional, more complete samples, but which all have smaller pinnules than the syntypes.

We have only seen *Cyathea acutidens* in the field in Colombia, but the description of the Costa Rican specimen *R.G. Wilson & C. Wilson 69-24* (UC) matches our observations, that the species occurs in dark wet spots in the forest and has basally tapering laminae.

Rojas-Alvarado (2007) considered *Cyathea leucolepismata* (as *Cyathea amazonica* R.C.Moran) to be conspecific with *Cyathea acutidens*, which would extend the range of the species along the eastern Andean slopes and into western Amazonia. This view is not followed here. First, the two species as we understand them have different ecological preferences, with *Cyathea acutidens* occurring mainly in dark humus rich gorges above 1100 m, whereas *C. leucolepismata* is a characteristic species of mineral soils (ranging from white sands to clayey soils), commonly found along rivers and trails where the light intensity is increased, mostly below 1000 m. At least in the Andes, the petiole scales of *C. acutidens* appear very broad, ovate and reach up to the central rachis where they can be long persisting (Fig. 3B); the petiole scales of *C. leucolepismata* appear narrow and lanceolate, and do not reach the rachis (Fig. 3E). The segment margins of *C. acutidens* are deeply incised so that each sorus almost sits on a separate lobe, and the margins are slightly revolute in fresh material so that they are usually folded in dried specimens; the margins of *C. leucolepismata* are comparatively less deeply incised and not revolute in fresh material, and thus mostly preserved in specimens in their flat natural position. See under *Cyathea lindigii* for further discussion.

2. *Cyathea columbiana* Domin, Pteridophyta: 263. 1929, *nom. nov.* for *Hemitelia obscura* Mett., Ann. Sci. Nat., Bot. sér. 5, 2: 264. 1864; not *Cyathea obscura* Copel., Philipp. J. Sci., C 4: 37. 1909. Type.—COLOMBIA. Nariño: "Prov. de Barbacoas, vía de Túquerres," 1600 m, 1 May 1852, *J.J. Triana s.n.* (lectotype, here designated: COL-000285370!; isolectotypes: B-

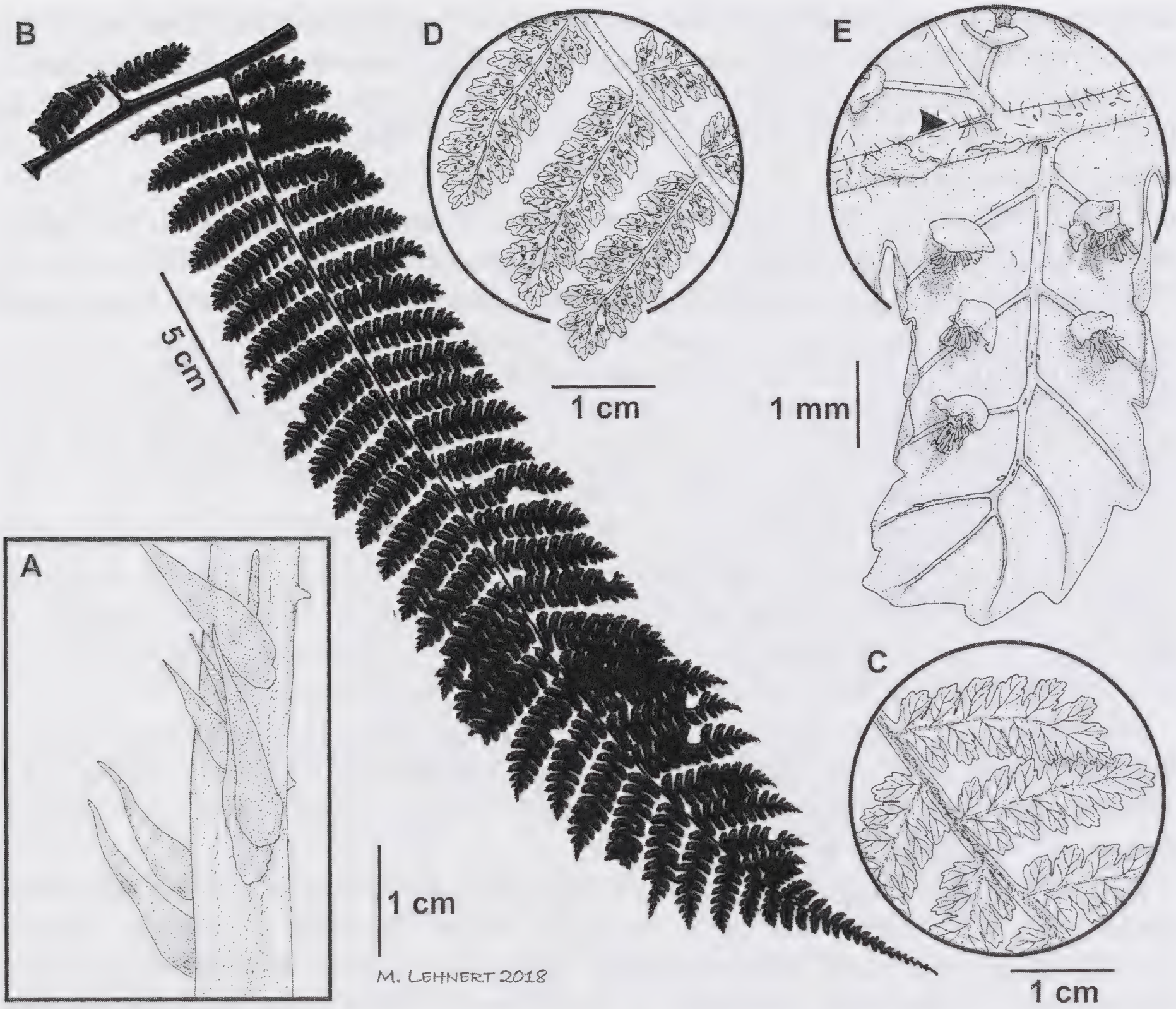

FIG. 4. *Cyathea columbiana*: A. Petiole with scales (*Croat & Gaskin 80935,* MO). B. Medial pinna, silhouette (*M. Lehnert 1582*, GOET). C. Green wings between pinnules in distal part of pinna (*Croat & Gaskin 80935,* MO). D. Pinnules, fertile, abaxially (*Croat & Gaskin 80935,* MO). E. Segment, fertile, abaxially; arrow points to acicular fungal fruiting bodies present on hair (*M. Lehnert 1582*, GOET).

20_0131284!, GH-00098052 [fragment of COL, image !], K-000589969!, NY-00148989!/-00148990 [fragment of K]!, P-00625703!). **Figs. 1C, 4, 5A–C.**

Trunks 0.8–2(–3) m tall, to 6 cm diam., with persistent old petioles, but these rotting off, hence trunk generally appearing untidy and irregularly thick (2.5–4 cm), sometimes with cleared areas showing leaf scars; trunk apex hidden in fascicle of petioles; adventitious buds absent. *Leaves* to 160 × 90 cm, expanding subsequently, held at an acute angle towards the trunk axis, ± planar, not arching. *Petioles* 30–50 cm long, inermous to sparsely aculeate, green to yellowish in young leaves, dark brown to brown in old ones, always matte, with one line of narrow white aerophores, each to 15 × 2 mm (shrunken and often inconspicuous in dried material); always matte, scurf a thin, amorphous layer consisting of pale to orange-brown branched hairs and lacerate squamules less than 1 mm long, soon shed. *Petiole scales* 15–20 × 2–5

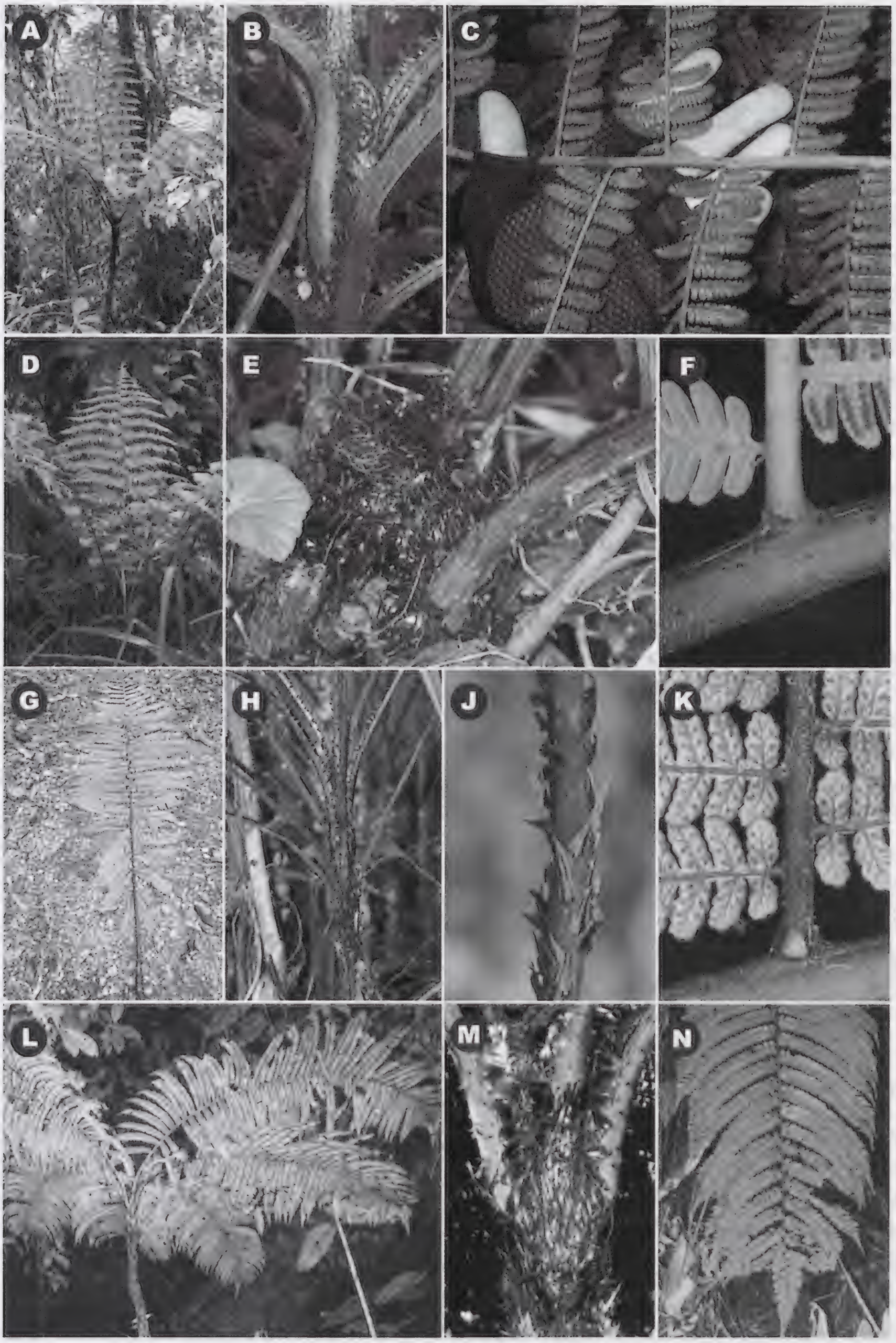

FIG. 5. Field characters. A–C. *Cyathea columbiana* (Pichincha, Ecuador; *M. Lehnert 1202*, photos M. Lehnert): A. Habit. B. Trunk apex. C. Center of leaf, adaxially. D–F. *Cyathea hildegardis* (Chocó, Colombia, photos E. Domínguez Vargas): D. Habit. E. Trunk apex. F. Costa and pinnule bases, abaxially. G–K. *Cyathea pinnuloides* (Chocó, Colombia, photos E. Domínguez Vargas): G. Leaf. H. Trunk apex. J. Detail of petiole with scales. K. Costa and pinnule bases, abaxially. L–N. *Cyathea uregoana* (Chocó, Colombia; photos A. Tejedor): L. habit. M. trunk apex. N. Leaf, distal half, showing abruptly reduced but non-conform apex.

mm, lanceolate, the apices weakly undulate, concolorous dark castaneous to weakly concordantly bicolorous with the margins paler brown to golden-brown, often abraded. *Rachises* inermous, green to brown, densely short pubescent adaxially, with reddish brown hairs to 1 mm long, antrorsely curved, less pubescent with paler, shorter hairs to glabrescent abaxially. *Laminae* 80–110 × 50–90 cm, long ovate, bipinnate-pinnatifid, apices gradually reduced, basal pinnae not or just weakly reflexed. Largest *pinnae* 36–45 × 4.5–6.5 cm; pinnae14–18 per leaf, sessile, alternate, patent, distally green-alate between the pinnules/segments (distal half if all pinnules sessile, distal third of pinnules stalked), apices attenuate. *Costae and costules* inermous, pubescent adaxially, the hairs antrorsely curved, 0.6–0.8 mm long, reddish brown on costae, becoming paler on costules, glabrous to glabrescent abaxially, often with ephemeral one-celled trichomidia. *Pinnules* to 21–35 × 9–12 mm, sessile or subsessile with stalks 1 mm long, linear-oblong to weakly oblanceolate, truncate to weakly cordate basally, obtuse to weakly acute apically. *Segments* weakly ascending, straight to weakly falcate distally, 4.0–5.0 × 2.4–3.2 mm, their margins serrate to dentate, glabrous adaxially except for one to two antrorsely curved multicellular hairs (0.5–1.0 mm long) on the midvein, abaxially with few flaccid white spreading hairs, inconspicuous, occasional with trichomidia (0.2 mm long) on and between veins, midveins also with small orange to brown, flattish to subbullate squamules to 0.5 mm long. Sterile veins simple, fertile veins simple, rarely forked. *Sori* 0.8(–1.0) mm diam., each with 30–40 sporangia, ± medial (few inframedial to subcostal), on the back of veins; indusia hemitelioid, brown, large, arching over the sori, more or less hemispherical, with subentire or slightly lacerate margins, reaching 1/3 around the receptacles, receptacles globose, 0.2–0.3 mm diam., paraphyses tan to brown, relatively thick, complanate, of the same length or slightly longer (ca. 0.3–0.4 mm) than the sporangia. Spores not examined.

Etymology.—The name refers to the country of origin of the type.

Distribution and habitat.—Colombia and Ecuador (Fig. 2B), endemic to the Chocó and Esmeraldas region on the wet western slopes of the Andes at 200–1600 m.

Additional specimens examined.—COLOMBIA. **Nariño:** Ricaurte, carretera entre Ricaurte y Altaquer, [ca. 3.8680806 N, 76.8191250 W] 1300 m, *L. Mora 3977* (COL). **Valle del Cauca:** Margen del Río Dagua, [ca. 1.2264583 N, 78.0647694 W] 200 m, 21 Dec 1967, *W. Hagemann 537* (COL).

ECUADOR. **Carchi:** border area between Prov. Carchi and Esmeraldas, about 30 km past Lita on road Lita - Alto Tambo, 450 m, 28 Jun 1991, *H. van der Werff et al. 12146* (MO, QCNE). **Esmeraldas:** between Lita and Alto Tambo, roadside and trails from road, 00°49′N, 78°27′W, 450–500 m, 16 Dec 2004, *M. Lehnert 1582* (GOET, QCA, UC); Lita - San Lorenzo road, 5.9 km from Lita, 07 Feb 1991, *R.C. Moran & C. Rohrbach 5341* (MO, QCNE, UC). **Los Ríos**: Quevedo, alrededores del Cerro Centinela, 10 km al W de Patricia Pilar, La Pirámide, 01°40′S, 79°20′W, 650 m, 25 Feb 1992, *G. Tipaz & C. Quelal 701* (MO, QCNE);

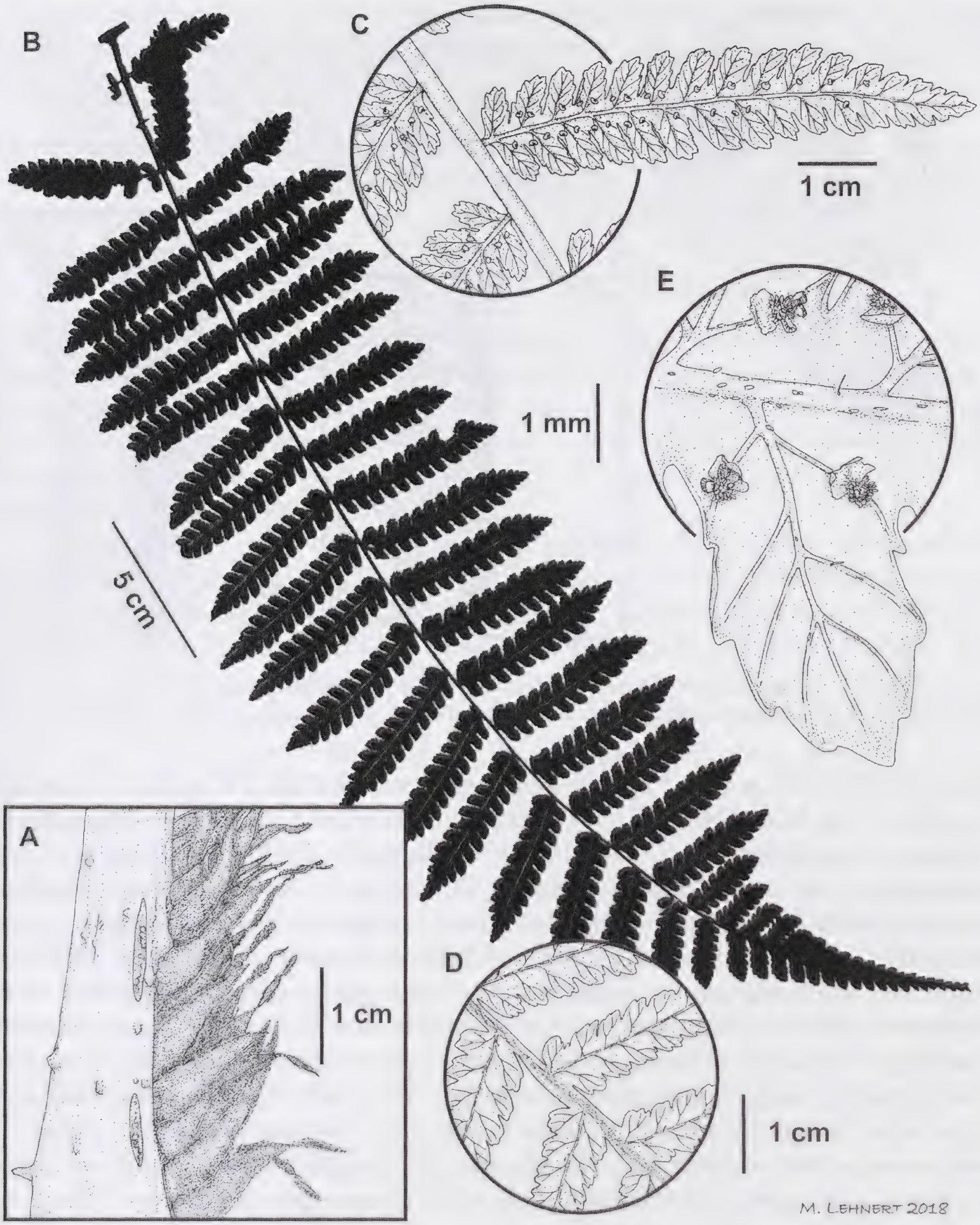

FIG. 6. *Cyathea austroamericana*: A. Petiole with scales. B. Medial pinna, silhouette. C. Pinnule, fertile, abaxially. D. Green wings between pinnules in distal part of pinna. E. Segment, fertile, abaxially (All drawn from, *Cafferty et al. 81A*, MO).

Summit of Cerro Samama (Hda. Clementina), S of road Caluma-Catarama, 01°40′S, 79°19′W, 700–730 m, 13–14 Nov 1996, *B. Øllgaard & H. Navarrete 2033* (AAU, QCA). **Pichincha:** Road El Paraiso - Saguangal, Km 2.9, 00°11′N, 78°46′W, 1400 m, 18 Feb 1995, *B. Øllgaard & H. Navarrete 857* (AAU, QCA); Reserva Maquipucuna, ca. 5 km (airline) ESE of Nanegal, Hda. El Carmen, trail

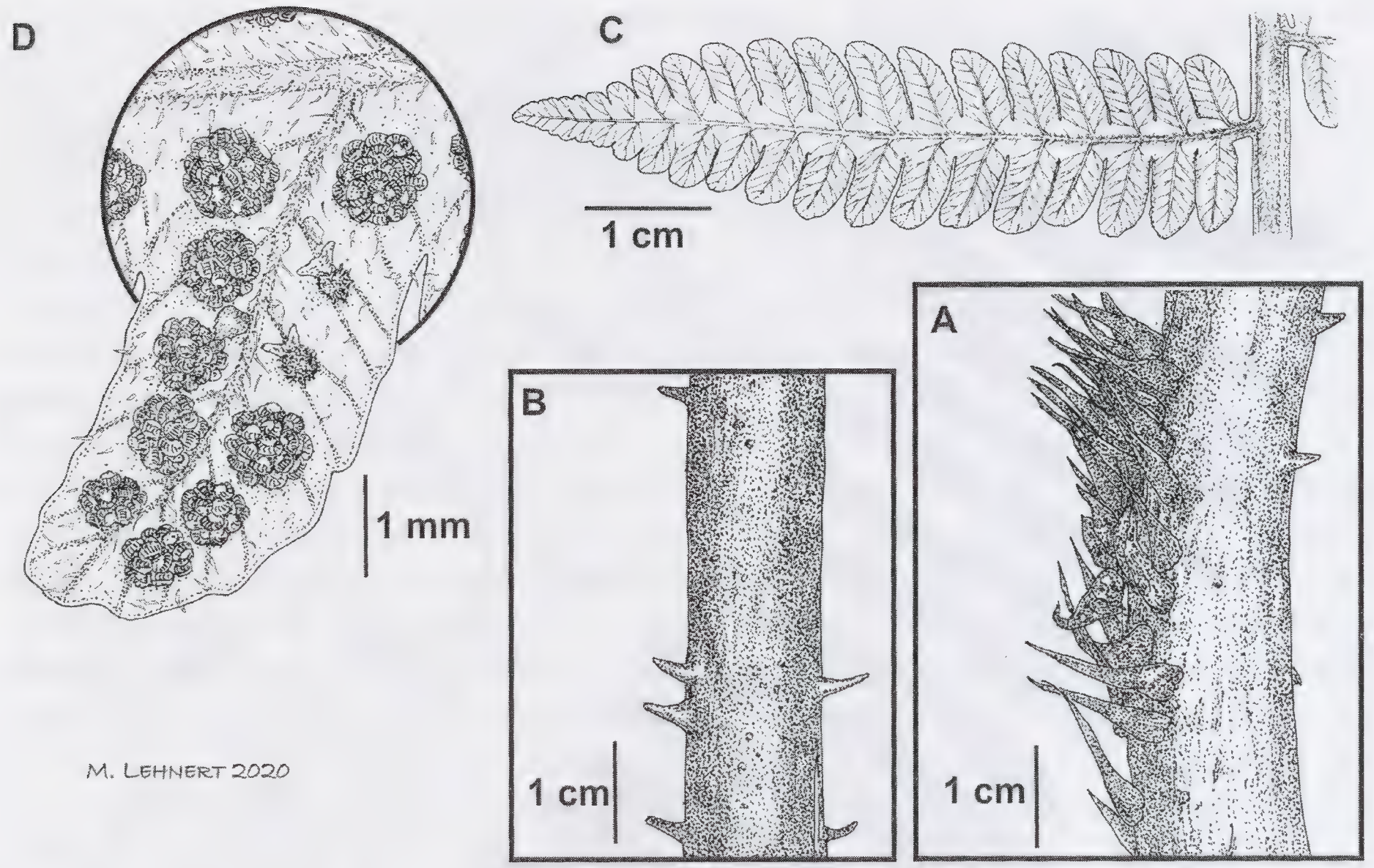

FIG. 7. *Cyathea hildegardis*: A. Petiole with scales. B. Part of lower rachis, abaxially. C. Pinnule, adaxially. D. Segment, fertile, abaxially. (All drawn from *F. Giraldo et al. 3752*, HUA).

along Río Umachca, just W of research station, 00°07′N, 78°38′W, 1250–1350 m, 28 Feb–04 Mar 1995, *B. Øllgaard et al. 936* (AAU, QCA); road Pacto-La Delicia-La Esperanza, Km 19.5, 00°11′N, 78°51′W, 1150 m, 01 Dec 1996, *B. Øllgaard et al. 2240* (AAU); Nanegal, Bosque Protector Maquipucuna, disturbed rain forest along trail from guard plantation Río Tumbi, 00°07.3′′N, 78°38′W, 1300–1400 m, 10 Jul 1992, *Webster & Deprete 29299* (AAU, QCNE).

Cyathea columbiana is most similar and geographically closest to *C. uregoana* (Fig. 4). Both species have notably small, blunt tipped pinnules resulting in a characteristic narrow linear pinna outline, which in turn ends in a long attenuate to caudate tip. Microscopically, both species have relatively large indusia that arch over the sori at least until the sporangia are shed. Both species are easily separated by the shape of the pinnae (Fig. 1) and the number of pinna pairs per leaf (14–18 in *C. columbiana* vs. more than 20 in *C. uregoana*).

As a herbarium specimen, *Cyathea columbiana* can be very similar to *C. austroamericana* (Fig. 5): both belong to the species with more consistently glabrescent to glabrous laminae and unforked fertile veins; other species of their size class (Figs. 1, 4) tend to be variously hairy and have both simple and forked fertile veins in the same leaf, *e.g.*, *C. multiflora*, *C. hildegardis* and *C. pinnuloides*. Older specimens lacking petiole scales had been regularly carried under their respective synonyms, *Hemitelia obscura* and *H. nigricans* C.Presl. With petioles, *C. austroamericana* can be easily separated by its darker, blackish petiole scales with ephemeral white margins.

Leaves of *Cyathea columbiana* are sometimes covered abaxially with black acicular fruiting bodies of a fungus, especially on thinner leaf axes, veins, and hairs.

3. ***Cyathea hildegardis*** Lehnert, F.Giraldo & W.D.Rodr., **sp. nov.** Type:—COLOMBIA. Chocó: Municipio Carmen del Atrato, en la vía a Quibdó, 05°46′17.1″N, 76°14′24.5″W, 1300 m, 12 Feb 2016, *F. Giraldo 3752 with A. Salino, E. Dominguez, I. Moura* (holotype: HUA-202771!/-202772!/-202773!; isotypes: BONN!, COL!, Z!). **Fig. 5D–F, 7.**

Diagnosis.—*Cyathea hildegardis* matches *C. pinnuloides* in being densely hairy on and between the veins abaxially but lacks strongly bullate squamules, which are substituted by flat ones with ciliate margins. *Cyathea hildegardis* also has larger, more acute pinnules than *C. pinnuloides*, in which they are conspicuously blunt, and has prostrate to ascending trunks, while *C. pinnuloides* always has erect trunks.

Trunks prostrate, to 8 cm diam., with persistent old petioles; adventitious buds absent. *Leaves* to 3.1 m long, arching from ascending petioles; expanding subsequently; covered abaxially with black acicular fruiting bodies of a fungus. *Petioles* to 80 cm long, with well-developed but rather scattered prickles to 3 mm long, green to grayish in young leaves, dark brown to brown in old ones, weakly shiny, scurf absent or scarce, consisting of scattered brown squamules, soon shed. *Petiole scales* 24–30 × 6 mm, broadly lanceolate, apices acute to attenuate, weakly undulate to weakly twisted, shiny, ± concordantly bicolorous dark castaneous with golden brown to yellowish margins. *Laminae* to 230 × 84 cm, long ovate to elliptic, bipinnate-pinnatifid, apices gradually reduced, with ca. 15 pinna pairs. *Leaf axes* [rachises, costae, and costules] with multicellular hairs, densely pubescent adaxially with hairs 0.5–0.7 mm long, tan and antrorsely curved; *rachises* abaxially dark reddish brown, with strong, long prickles especially in lower half, rachises abaxially glabrescent with flaccid whitish hairs to 2 mm long. Largest *pinnae* 38–42 × 10 cm, sessile to stalked to 0.5 cm, alternate, patent to weakly ascending, apices acute to attenuate; basal pinnae almost as long as longest pinnae, patent to weakly reflexed. *Costae* inermous, or weakly scabrous, 1.5–2.0 mm wide, green on both sides or yellowish brown abaxially, distally broadly green-alate between the pinnules/segments; junctures of costae and rachises not or weakly swollen abaxially, each with a planar to weakly raised pneumathode, to 2 × 1 mm, often black in dried specimens. Largest *pinnules* 50 × 10–12 mm, pinnules mostly sessile, oblong, bases truncate to weakly cuneate, tips short-acute; costules abaxially with few orange-brown to orange squamules 0.5–1.0 mm long, mainly flat, few sub-bullate, with long marginal cilia; costules pale green on both sides, basally without pneumathodes. *Costules* yellowish brown, hairy on both sides, hairs like on costae or veins. *Segments* to 7 × 2 mm, ascending, straight or weakly falcate distally, their margins dentate-crenate or serrate; sinuses acute, narrow, to 0.5 mm wide; adaxially with few antrorsely curved yellowish hairs (0.5–1.0 mm long) on the midveins, densely hairy

abaxially with erect, white, multicellular hairs to 1.0 mm long on and between the veins, veins also with appressed white trichomidia, with orange-brown to orange squamules 0.5(–1.0) mm long, mainly flat, few sub-bullate with subulate tips. Sterile veins simple, fertile veins simple, rarely forked. *Sori* 0.8 mm diam., medial; indusia hemitelioid, often split to a fish-tail form, tan to brown, reaching 1/4 or less around the receptacles, obscured in entire sori; receptacles globose, 0.2(–0.3) mm diam., paraphyses tufted on receptacles, whitish to tan, bases turgid, apices catenate, of the same length as sporangia (0.4–0.5 mm). *Spores* not examined.

ETYMOLOGY.—The name commemorates Hildegard Hass (1933–2018), grandmother of author M. Lehnert.

DISTRIBUTION AND HABITAT.—Northwestern Colombia (Chocó) (Fig. 2C) in wet lower montane forests at 1300 m. Only known from the type population.

The type population of *Cyathea hildegardis* consists of few plants with prostrate trunks and erect leaves found in a clearing. It is not known if this habit is due to some external factor (like flattening by strong winds) or if it is a genetically fixed character of this Andean population. Prostrate trunks are known from several other taxa of the *C. multiflora* group: *Cyathea squarrosa*, a species from Costa Rica, can be distinguished by the presence of bicolorous scales with white margins reaching from the petiole base up to the central rachis; *Cyathea mariposana* sp. nov. (described herein) from Panamá has uniform brown petioles scales like *C. hildegardis* but has the sori closer to the segment margin and less armed petioles than that species.

Cyathea pinnuloides more or less matches *C. hildegardis* in pinnule size and shape *(i.e.*, parallel-sided with blunt segment tips but clearly pointed apex) but differs in having undivided indusia (vs. formed like fish tails in *C. hildegardis*). Both are further similar regarding the indument on the abaxial side of the lamina, as both have hairs on costae, costules, on and between the veins, with weakly bullate and flat squamules present.

4. *Cyathea leucolepismata* Alston, J. Wash. Acad. Sci. 48: 231. 1958. Type.—COLOMBIA. Putumayo: Near San Diego de Colorado, between Umbria and Puerto Asís, 16 Jan 1945, *J.A. Ewan 16784* (holotype: BM-000937685!/-000937686!; isotypes: MICH-1191237 [image seen], NO-0109709 [image!], P-00625699 [image!], S-R-1357!, UC-1077956!, US-00066155!/-00066156!/-00066157!, VEN-170671[image !]). **Figs. 3D–J, 8.**

Cyathea amazonica R.C.Moran, Nordic J. Bot. 15: 53. 1995. Type.—ECUADOR. Napo: Upper Río Tiputini, ca. 2 h from bridge on Coca-Auca oilfield road, 00°43′S 76°57′W, 300 m, 21 Jul 1991, *B. Øllgaard & M. Blasco 99065* (holotype: AAU!; isotypes: K n.v., LPB-0000037!, QCA!, QCNE-164!, U-0007586 [image!], UC-1605833!, US-00512902!).

Trunks to 4 m tall, 6–11(–15) cm diam., covered with old petiole bases, due to these often spiny; apices hidden between petiole bases; without adventitious buds. *Leaves* to 300 cm long, erect, unfolding only one at a time; dead

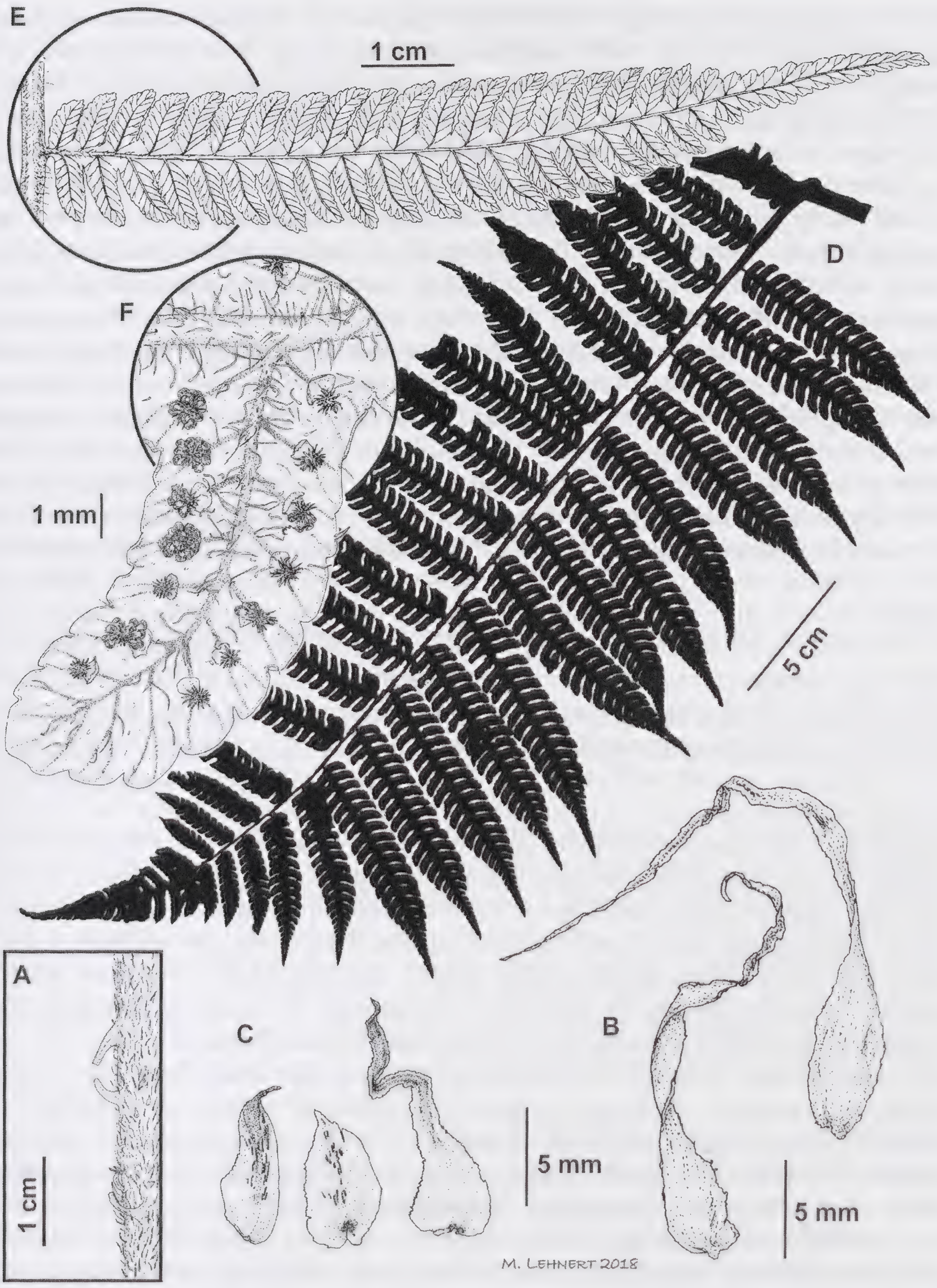

FIG. 8. *Cyathea leucolepismata*: A. Petiole with hairs (*M. Lehnert 2829*, BONN). B) Larger petiole scales (*M. Lehnert 2829*, BONN). C. Smaller scales from axils between rachis and costa (*M. Lehnert 2829*, BONN). D. Medial pinna, silhouette (*Ewan 16784*, isotype COL). E. Pinnule, adaxially (*M. Lehnert 74*, GOET). F. Segment, fertile, abaxially (*M. Lehnert 2829*, BONN).

leaves sometimes forming a skirt below the crown. *Petioles* to 110 cm long, usually strongly aculeate with prickles 3–10 mm long, dark reddish brown to blackish, rarely dark grayish brown, matte, with many erect, tan to white hairs 2–3 mm long and many appressed unicellular trichomidia mostly without scaly scurf, rarely some scattered whitish erect lanceolate squamules to 2 mm long near the base; petioles basally with a discontinuous line of pneumathodes to 10.0 × 0.5–1.0 mm on each side, white in fresh material, orange-brown and inconspicuous in dried material. *Petiole scales* long-lanceolate, to (15.0–)20.0–35.0 × 3.0–5.0 mm, rather thin textured, usually twisted, proximal ones discordantly bicolorous ochre to pale, rarely shiny dark brown with stramineous to whitish margins, distal ones almost concolorous stramineous to white with a basal dark brown spot, some also with a dark brown streak in their tip; differentiated margins without setae or colored teeth, fragile, usually fragmented. *Laminae* to 200 × 120–150 cm, bipinnate-pinnatifid, firm herbaceous, matte, dark-green adaxially, paler green abaxially; apices gradually reduced to abruptly reduced to non-conform apical section. *Rachises* inermous to sparsely short-aculeate proximally, dark reddish brown adaxially, dark stramineous to pale grayish brown abaxially, often mottled brown to reddish brown; densely pubescent with multicellular hairs 1.0–1.5 mm long, tan to brown and antrorsely curved adaxially, white to tan and spreading abaxially. Largest *pinnae* 65–75 cm long, sessile to stalked to 1.5 cm, patent to weakly ascending, 10–12 pairs per leaf, alternate, inarticulate, distally narrowly to broadly green-alate, distal segments simply adnate before ending in a pinnatifid apical section; basal pairs ca. 3/4 the length of the medial pinnae, notably reflexed. *Costae* 2.5–3.0 mm wide, inermous to sparsely verrucate, dark orange-brown to grayish brown abaxially, dark yellowish to reddish brown adaxially; densely pubescent with multicellular hairs 1.0–1.5 mm long, tan to brown and antrorsely curved adaxially, white to tan and spreading abaxially; junctures of costae and rachises weakly swollen on both sides, abaxially often black when dried, bearing each a planar elliptic pneumathode to 2.0–3.0 × 1.0 mm, gray-brown to blackish, conspicuous. Largest *pinnules* 85–120 × (14–)20–30 mm, sessile to subsessile with stalks to 2 mm, inarticulate, (1.1–)1.5–2.5(–3.5) cm between the stalks/costules, linear-oblong to lanceolate or long triangular, truncate to weakly cordate basally, long-acuminate to long attenuate apically with serrate to crenulate margins; costules yellowish to grayish brown adaxially and abaxially, proximally often darker brown, strongly prominent, ridged, and densely hairy adaxially with tan to brown, curved multicellular hairs to 1.0 mm long, abaxially weakly prominent, densely hairy with erect, white, stout multicellular hairs to 1.5 mm long, also with some white to basally tan squamules, bullate ones to 0.8–1.0 mm long, flat lanceolate ones to 3 × 2 mm, with entire margins and short-attenuate tips. *Costules* basally without pneumathodes, but often with a black spot abaxially in dried specimens. *Segments* 9.0–17.0 × 3.0–5.0 mm, sessile, adnate, rarely remote and then connected by laminar tissue, patent to strongly ascending, distally falcate, tips obtuse to acute, proximal segments alternate to subopposite, usually a bit shorter than following segments; sinuses acute to

obtuse, to 1.0–2.0 mm wide; margins crenate-dentate to serrate, *i.e.*, each fork of a lateral vein ends in a separate marginal lobe; margins not differently incised in proximal segments of a pinnule; veins planar on both sides or weakly protruding adaxially, dark yellowish to grayish brown; veins adaxially glabrous except for some multicellular hairs to 0.5 mm long on the midveins, abaxially hairy with many erect to curved, white multicellular hairs to 1.0–1.5 mm long, also between the veins; midveins with some pure white to basally tan squamules, mostly bullate ones to 1.0 × 0.5 mm; sterile veins simple or forked, fertile veins forked. *Sori* (0.8–)1.0 mm diam., each with ca. 20–30 sporangia, medial to supramedial, in the fork of veins, immature pale whitish-yellow, mature dark orange-brown; indusia hemitelioid, reaching 1/4 to 1/3 around the receptacles, glabrous, yellowish brown to white, matte, firm, margins with shallow lobes, appressed to ascending but not arching over sori, completely covered by intact sori; indusia usually preserved in over-mature sori; receptacles globose to weakly columnar, 0.3–0.4 mm diam., paraphyses numerous, flaccid, hyaline, white to tan, much longer than the sporangia (0.5–0.6 mm long), sometimes broken off to the darkened bases. Spores not examined.

Etymology.—The name refers to the white scales found on the lamina and the upper petiole parts.

Distribution and habitat.—Colombia, Ecuador, Peru, and Bolivia (Fig. 2), to be expected in western Brazil (Amazonas & Acre state), in lower montane forests and Amazonian lowlands at 90–1300 m.

Additional specimens examined.—COLOMBIA. **Amazonas:** Puerto Nariño and vicinity on Río Amazonas near mouth of the Río Loretoyacu, [ca. 03°47′03.1″S, 70°21′49.1″W, 50–100 m] 04 Mar 1975, *J.L. Zarucchi & R.E. Schultes 1048* (GH). **Caquetá:** San José del Fragua, Inspección de policía de Puerto Bello, margen izquierda del Río Fragua, Vereda La Argentina, puente divisorio limite entre Caquetá y Cauca, 01°08′40.6″N, 76°16′08.5″W, 200 m, 10 Nov 2015, *F. Giraldo 3634* (HUA), ibid., 10 Nov 2015, *F. Giraldo 3683* (HUA). **Vaupes:** Río Apaporis, entre el río Pacoa y el río Kananari, Soratama, 250 m, 20 Aug 1951, *R.E. Schultes & I. Cabrera 13652* (GH).

ECUADOR: **Napo:** Experimental station of INIAP, San Carlos, 6 km SE of Los Sachas, 250 m, 19 Apr 1985, *M.A. Baker & N. Trushell 6094* (UC); Along road between Baeza and Archidona, 16 km S of turn off to Loreto and Cocoa, 00°46′56″S, 77°46′51″W, 985 m, 19 Apr 2003, *T.B. Croat, L. Hannon & N. Altamirano 87815* (QCNE); Río Cuyabeno, near Puerto Montufar, 00°06′S, 76°01′W, 230 m, 17 Feb 1980, *L. Holm-Nielsen, J. Jaramillo, J. Brandbyge 21289* (QCA); Cantón Napo, near Archidona, 650 m, 23 Apr 1935, *Y. Mexia 7318* (UC); Parque Nacional Yasuní, estación Cientifica Yasuní, por el Río Tiputini, transect 1, 1 km E of the biological station, 00°04′05″S, 76°28′W, 200 m, 10 Apr 1996, *R.C. Moran, H. Tuomisto, K. Ruokolainen, A. Poulsen 6045* (QCA); Parque Nacional Yasuní, km 38.8 on Maxus Energy road, transect 23, 00°40′S, 76°27′W, 21 Apr 1996, *R.C. Moran, H. Tuomisto, K. Ruokolainen, A. Poulsen*

6277 (QCA); Río Tupitini, E of Puerto Colón, 08 May 1991, *B. Øllgaard 98953* (AAU); Anangu, 00°31–32′S, 76°23′W, 260–350 m, 30 May–21 Jun 1982, *B. Øllgaard, J. L. Luteyn, S. A. Mori, B. Boysen Larsen, B. Boom, & A. R. Jensen 39215* (QCA, UC). **Pichincha:** Sanguangal, Hacienda Conquista, water catchment reserve ca. 2 km S of Hacienda, 770–820 m, 09–12 May 1995, *B. Øllgaard, H. Navarrete, C. Kragelund, & H. Ankersen 1101* (AAU, QCA). **Sucumbios:** Sinague, upstream from Umbaqui on Río Aguarico, ca. 2.3 km NW of village near Río Candué, 00°06′S, 77°26′W, 620 m, 23 Oct 1996, *B. Øllgaard & H. Navarrete 1845* (AAU, QCA). **Zamora-Chinchipe:** along road from near Paquisha S to Las Orquideas and end of the road on Río Nangaritya vía Guazyimi, beginning 15.9 km E of Yzumbi and Río Zamora, then 46.9 km S at Las Orquideas, 04°13′44"S, 78°39′30"W, 877 m, 16 Jul 2004, *T.B.Croat, L. Hannon, G. Walhert, & T. K. Jua 91267* (MO); Lodge "Copalinga", 3 km from Bombuscaro Ranger Station of Podocarpus National Park, 900–1300 m, 15 Sep 2004, *M. Lehnert 1249 with M. Kessler* (GOET, QCA, UC); Shaime, at junction of Río Nagaritza and Río Numpatakai, 04°22′S, 78°42′W, 1000–1080 m, 07 Dec 1990, *B. Øllgaard 98436* (AAU, QCA); Miazi, at junction of Río Chumbiriatza with Río Nangaritza, 04°19′S, 78°40′W, 950–1200 m, 21–23 Oct 1991, *B. Øllgaard, B. Bergmann, & M. Ruíz 99373* (AAU, QCA); Río Nangaritza, trail along river S of La Wanta, 14 km SE of Guayzimi, 04°09′S, 78°38′W, 900 m, 13 Nov 1997, *B. Øllgaard & P. Lozano 2584* (AAU, QCA).

PERU. **Cuzco:** La Convención, Distrito Echaratí, San Martin-3 well site, 11°46.89′S, 72°42.10′W, 400 m, 15 Feb 1997, *P. Nuñez et al. 19143* (USM); *ibid.*, 11°46′53.5"S, 72°42′06"W, 400 m, 10 Mar 1997, *P. Nuñez 19340* (US); *ibid.*, Pagoreni well sites, 11°41′S, 73°00′W, 350 m, 18 Apr 1998, *P. Nuñez, W. Nauray, L. Acurio, R. de la Colina, N. Llerena, & A. Salas 21682* (USM). **Loreto:** Mariscal Ramón Castilla, Río Zavari, 65 km down the river from Angamos, half distance to mouth of Río Yawari Mirin, Quebrada Buenavista, 04°50′04"S, 72°23‘25"W, 90–150 m, 05 Apr 2003, *H. Beltrán, R. Foster, N. Pitman, R. Garcia, C. Vriesendorp, & M. Huite 5549* (UC); Gamitanacocha, Río Mazán, 100–125 m, 25 Jan 1935, *J.M. Schuncke 117* (UC); Maynas, between the roads Ex Petroleros and Bello Horizonte, Km 38–40 of the road Iquitos-Nauta, 04°04′S, 73°28′W, 100–200 m, 06 Jan 1995, *H. Tuomisto, K. Ruokolainen , A. Sarmiento, & J. Järvinen 6674* (UC); ibid., 06 Jan 1995, *H. Tuomisto, K. Ruokolainen, A. Sarmiento, & J. Järvinen 6677* (GOET, TUR); Maynas, Distrito Sargento Lores, Constancia Norte, 04°07′19″S, 72°55′25″W, 116 m, 11 Apr 1997, *Vasquez R., Phillips O., Rojas R., & A. Penha 22868* (UC). **Madre de Dios**: Manu, Parque Nacional Manu, Río Manu, Río Sotileja, 11°40′S, 71°55′W, 400–500 m, 04 Oct 1986, *R.B. Foster & B. D'Achille 11627* (UC); Manu, close to the village of Diamante, S side of Río Alto Madre de Dios, 12°20′S, 70°57′W, 400 m, 24 Oct 1998, *H. Tuomisto, K. Ruokolainen, & A. Zegarra 13394* (UC); Tambopata, E bank of Río del los Amigos, 10 km upriver from its mouth, 12°29′S, 70°10′W, 200–300 m, 08 Nov 1998, *H. Tuomisto, K. Ruokolainen, & A. Zegarra 13655* (UC).

BOLIVIA. **Beni:** Prov. Ballivian, Pilon Lajas, camino del poste de ENTEL entre Porvenir y Puente Río Quiquibey, 15°09′S, 67°04′W, 1150 m, 01 Oct 2000,

M. Lehnert 74 (LPB); Lower slopes of Serrania Pilon Lajas, 14.3km N of the bridge over Río Quiquibey, 15°19′S, 67°03′W, 700 m, 10 Jun 1985, *J.C. Solomon 13955* (LPB, MO, UC); Ichilo, Parque Nacional Amboró, Río Yapojé y Saguayo, 8 km al SW de la localidad El Carmen, 17°33′30"S, 63°44′W, 360 m, 15–22 Nov 1991, *I. Vargas & T. Killeen 1217* (MO, UC). **La Paz:** Prov. Abel Iturralde, Alto Madidi across from mouth of Río Enlatagua, Transect 1, 13°35′S, 68°46′W, 280 m, 21 May 1990, *A. Gentry & S. Estensoro 70236* (LPB, MO); ibid., Transect 6, 13°35′, 68°46′W, 280 m, 22 May 1990, *A. Gentry & S. Estensoro 70366* (MO, UC), ibid., Transect 9, 13°35′S, 68°46′W, 280 m, 23 May 1990, *A. Gentry & S.Estensoro 70434* (LPB, MO), ibid., Transect 10, 13°35′S, 68°46′W, 280 m, 23 May 1990, *A.Gentry & S. Estensoro 70465* (LPB, MO); Prov. Franz Tamayo, Parque Nacional Madidi, Virgen del Rosario, Chaquisapa, 13°29′11.9"S, 68°24′49.4"W, 920 m, 8 Nov 2003, *L. Cyaola 453* (LPB, UC); 42km al W y 1km al N de Rurrenabaque, 14°25′S, 67°55′W, 330m, 05 Oct 1994, *N. Helme 235* (LPB); Prov. Sud Yungas, Sapecho; Colonia Tupiza B, ca. 3 h a pie de Sapecho, 15°31′S, 67°18′W, 950 m, 14 Apr 2003, *M. Lehnert 770* (GOET, LPB, UC); ladera occidental de la Serrania Marimonos, 15°30′S, 67°19′W, 600 m, 09 Jul 1992, *R. Seidel 5792* (LPB); Prov. Alto Beni, Colonia Tarapacá, 15°32′S, 67°22′W, 600 m, 24 Nov 1993, *R. Seidel 7466* (LPB). **Santa Cruz:** Prov. Ichilo, Parque Nacional Amboró, along Quebrada Yapojé and Quebrada Esperanza, 2 km upstream from confluence with Río Saguayo, 17°35′S, 63°45′W, 375 m, 12 Jun 1991, 12 Jun 1991, *M. Nee 40929* (LPB, MO); Parque Nacional Amboró, arroyo Rududi, along Río Tuichi, 362 m, 29 Sep 2001, *N. Paniagua et al. 4866* (LPB, UC); Velasco, Parque Nacional Noel Kempff M., Campamento Huanchaca 1, 13°54′S, 60°48′W, 650 m, 18 May 1994, *L. Arroyo & T. Killeen 714* (UC).

Cyathea leucolepismata would have been better suited with its synonym, *C. amazonica*, because it can be found only in the Amazon basin, most commonly in the foothills of the neighboring Andes but also in terra firme forest in the Amazonian lowlands. The distinction from the Guayana shield endemic *C. boryana* (Kuhn) Domin is still contentious because only few collections of that species are available. That species also has pale petiole scales, spiny petioles and rachises, and hemitelioid indusia, but is much less hairy with shorter hairs, and the indusia are paler. All that is known of its ecology is that it prefers wet conditions and can grow on laterite outcrops, which overlaps with the known ecological amplitude of *C. leucolepismata*. If both names represent only one species, *C. boryana* would have priority over *C. leucolepismata*.

Both *Cyathea leucolepismata* and *C. boryana* are very similar in habit and indument to the exindusiate *Cyathea leucofolis* Domin from SE Brazil but can be easily separated by their hemitelioid indusia.

5. *Cyathea lindigii* (Baker) Domin, Pteridophyta: 264. 1929. *Hemitelia lindigii* Baker, Sp. Fil. 454. 1874. Type.—COLOMBIA. Cundinamarca: Alto del Trigo, Andes of Bogotá, *A. Lindig 310* (holotype: K-000575410!/-000575411!; isotypes: P-00625701!/-00625702!, GH [photo P, image!]). **Figs. 1E, 9.**

Trunks 1–4(–10) m tall, 6–15 cm diam. (reports of 25–30 cm diam. presumably included the investing sheath of adventitious roots), covered with old petiole bases, due to these generally spiny; apices hidden between petiole bases; without adventitious buds. *Leaves* to 300 cm long, erect, unfolding several at a time; dead leaves sometimes forming a skirt below the crown. *Petioles* 50–150 cm long, usually strongly aculeate with spines to 5 mm long, dark reddish brown to blackish, rarely dark stramineous, opaque, glabrous or glabrescent with many tan, appressed trichomidia to 0.2 mm long, rarely with white appressed squamules at the very base, to 1 mm long with long hair-like apices and entire margins; hairs absent; petioles basally with a discontinuous line of distant pneumathodes to 7.0 × 2.0 mm on each side, white in fresh material, grey brown and inconspicuous in dried material. *Petiole scales* long lanceolate, (15.0–)25.0–35.0 × 2.5–4.0 mm, rather thinly textured, usually twisted, proximal ones concordantly to discordantly bicolorous, auburn to dark brown with whitish margins, on distal petiole parts sometimes gradually becoming paler; differentiated margins without setae or teeth, fragile, usually fragmented; scales covering the croziers auburn to reddish, almost concolorous or with very narrow, often abraded, whitish to yellowish margins. *Laminae* to 180 × 120–140 cm, bipinnate-pinnatifid, firm herbaceous, matte, dark-green adaxially, paler green abaxially; apices gradually reduced. *Rachises* inermous to sparsely short-aculeate proximally, dark stramineous to pale grayish brown abaxially, dark reddish brown adaxially; with tan to brown multicellular hairs 1.0–1.5 mm long, antrorsely curved and persistent adaxially, spreading and worn off with age abaxially, leaving the cortex smooth or scabrous. Largest *pinnae* 65–75 × 17–30 cm, subsessile to stalked to 3 cm, patent to weakly ascending, alternate, inarticulate, distally narrowly to broadly green-alate, distal segments simply adnate before ending in a pinnatifid apical section; basal pairs smaller than the medial pinnae, notably reflexed. *Costae* 2.5–3.0 mm wide, inermous to sparsely verrucate, dark orange-brown to grayish brown abaxially, dark yellowish to reddish brown adaxially; with multicellular hairs 1.0–1.5 mm long, densely pubescent adaxially with hairs tan to brown and antrorsely curved, sparsely pubescent and glabrescent abaxially with hairs white to tan and spreading; junctures of costae and rachises weakly swollen on both sides, abaxially often black when dried, without distinct aerophore, but sometimes with small gray, pock-like outgrows. Largest *pinnules* 85–150 × (14–)20–30 mm, sessile to short-stalked to 2 mm, articulate, 1.5–2.0(–2.2) cm between the stalks/costules, linear-oblong to oblanceolate, truncate to weakly cuneate basally, long-acuminate to long attenuate apically with serrate to crenulate margins. *Costules* yellowish to grayish brown adaxially and abaxially, proximally often darker brown, strongly prominent, ridged, and densely hairy adaxially with tan to brown, antrorsely curved multicellular hairs to 1.0 mm long, abaxially weakly prominent, glabrous or glabrescent with appressed, tan to brown unicellular trichomidia; also with some white to basally tan squamules, bullate ones to 0.8–1.0 mm long, flat lanceolate ones to 3 × 2 mm, with entire margins and short-attenuate tips; costules basally without pneumathodes, but often with a black spot or line (abscission layer)

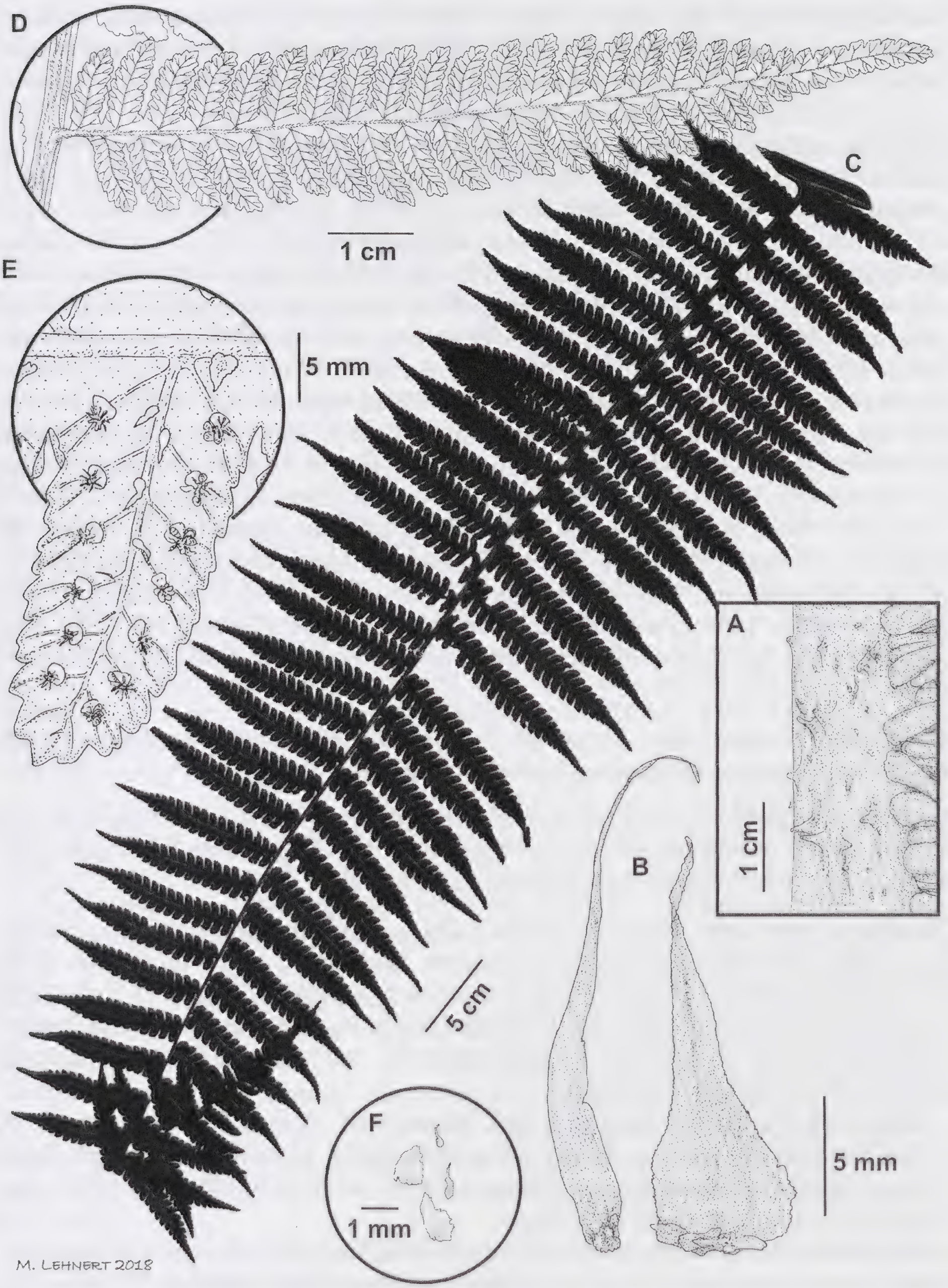

FIG. 9. *Cyathea lindigii*: A. Petiole, (*M. Lehnert 54*, GOET). B. Petiole scales (*D.N. Smith 6558*, MO). C. Medial pinna, silhouette (*A. Lindig 310*, isotype P). D. Pinnule, adaxially (*M. Lehnert 40*, GOET). E. Segment, fertile, abaxially (*A. Lindig 310*, isotype P). F. Laminar squamules (*A. Lindig 310*, isotype P).

abaxially in dried specimens. *Segments* to 7.0–13.0 × 3.0–4.5 mm, sessile, adnate, rarely remote and then connected by laminar tissue, patent to strongly ascending, distally falcate, tips usually acute, sometimes obtuse, proximal segments alternate to subopposite, usually a bit shorter than following segments; sinuses acute to obtuse, to 1.0(–2.0) mm wide; margins crenate-dentate to serrate; margins not differently incised in proximal segments of a pinnule; veins planar on both sides or weakly protruding adaxially, dark yellowish to grayish brown; veins adaxially glabrous except for some multicellular hairs to 0.5 mm long on the midveins, abaxially midveins with some pure white to light brown squamules, mostly bullate ones to 1.0 × 0.5 mm, hairs absent, rarely with trichomidia or scattered white hairs to 0.5 mm long; sterile and fertile veins simple or forked. *Sori* 0.8–1.0 mm diam., supramedial (appearing inframarginal if lobes of segments are revolute), in the fork or on the back of veins, immature pale whitish-yellow, mature dark orange-brown; indusia hemitelioid, reaching to 1/4 around the receptacles, usually brown, rarely yellowish to whitish, matte, firm, margins with shallow lobes, appressed to ascending but not arching over sori, completely covered by intact sori; indusia usually preserved in over-mature sori; receptacles globose to weakly columnar, 0.2–0.3 mm diam., paraphyses few to numerous, stiff, hyaline, tan to brown, as long as or shorter than the sporangia (0.3-0.4 mm long). *Spores* tetrahedral-globose, pale yellow; perispore and exospore not examined.

Etymology.—Named after Alexander Lindig (1815–1882), plant collector, who made extensive collections in Colombia from 1859–1863.

Distribution and habitat.—Central and eastern Cordillera of Colombia (Fig. 2C) at 1300–2200 m and the eastern Andean foothills of Peru and Bolivía at 280–1300 m, in moist premontane and montane forests.

Additional specimens examined.—COLOMBIA. **Cundinamarca:** Albán, vereda Las Marias, Fundación Granjas Infantiles del Padre Luna, Granja del Gran Ciudadano, 1900 m, 10 Nov 2011, *Triana-M. & Murillo 105* (COL); ibid., 2200 m, *Triana-M. & Murillo 037* (COL). **Huila:** Mun. Palermo, vereda El Boquerón-Diamante, 02°50′39.4885″N, 75°33′50.5957″W, ca. 1500 m, 09 May 2015, *C. Barbosa & A. Garcia F002* (COL).

PERU. **Junin:** Satipo, Gran Pajonal, Mapari, ca. 12 km SW of Chequitavo, 10°45′S, 74°23′W, 1300 m, 7 Apr 1984, *D.N. Smith 6799* (USM); Satipo, Gran Pajonal, between Paucarete and Tihuanaski, 10°45′S, 74°23′W, 1200 m, 29 Mar 1984, *D.N. Smith 6558* (MO, USM).

BOLIVIA. **Beni:** Ballivián, 25 km from Yucumo on Yucumo - Quiquibey road, in the Pilón Lajas, 15°17′S, 67°04′W, 950 m, 17 Jul 1990, *A. Fay & L. Fay 2743* (LPB, MO, US), ibid., 17 Jul 1990, *A. Fay & L. Fay 2754* (LPB, MO, US); Río Chimane - Environs of Fatima, ca. 14°40′S, ca. 66°20′W, 728 m, 29 Mai 1982, *E.W. Davis 1071* (F, GH, LPB); 16 km por el camino maderero, al SW del km 12 Yucumo - Rurrenabaque, 15°05′S, 67°07′W, 800 m, 3 Aug 1997, *M. Kessler, J. Gonzales, K. Bach 10974* (LPB, UC). **Cochabamba:** Carrasco, Parque

Nacional Carrasco, al S del campamento petrolero Ichoa, 17°23′S, 64°24′W, 530 m, 19 Sep 1997, *A. Acebey 657* (LPB, UC); Ayopaya, cruzando el río Ipiri, subiendo a la cima de la serranía de Mosetenes, ladera superior, 16°03′S, 66°41′W, 1112 m, 21 Sep 2004, *H. Huaylla 1335* (GOET, LPB, UC); Ayopaya, subiendo hacia la cima en dirección del sub campamento, 16°02′S, 66°39′W, 1105 m, 24 Sep 2004, *H. Huaylla 1405* (GOET, LPB); Carrasco, Campamento Guacharos, pasando el río San Mateo hacia lagunillas, en los alrededores, 17°05′74″S, 65°27′85″W, 600 m, 11 Dec 1999, *I. Jiménez 54* (AAU, LPB), *56* (AAU, LPB), & *61* (AAU, LPB); *ibid.*, 600 m, 12 Dec 1999, *I. Jiménez 80* (AAU, LPB), *89* (AAU, LPB), *& 96* (AAU, LPB); Carrasco, ca. 15 km al sur del pueblo de Sacta, en dirección al Río Leche, 17°16′75″S, 64°45′76″W, 520 m 21 Jan 2000, *I. Jiménez 255*(AAU, LPB); alrededores del punto 15, en el límite del Parque N. Carrasco con Nueva Jerusalem, 17°15′20″S, 64°48′65″W, 400 m, 20 Jan 2000, *I. Jiménez* 246 (AAU, LPB); Chapare, El Palmar, 155 km antigua carretera Cochabamba - Villa Tunari, 17°05′S, 65°32′W, 750 m, 4 Sep 1996, *M. Kessler, J. Gonzales, T. Krömer 8120* (LPB, UC); Chapare, Cavernas de la Repechón, PN Carrasco, 17°02′S, 65°26′W, 550 m, 8 Sep 1996, *M. Kessler, J. Gonzales, T. Krömer 8302* (LPB, UC); Chapare, Villa Tunari, Terreno del Hotel "El Puente", 16°58′S, 65°45′W, 550 m, 29 Aug 2000, *M. Lehnert 40* (GOET, LPB, UC), camino al Hotel "El Puente", 16°58′S, 65°45′W, 600 m, 30 Aug 2000, *M. Lehnert 45* (GOET, LPB, UC); Chapare, entre Villa Tunari y Cochabamba, km 351, cerca del restaurante "Lagunitas" y el Río Antahuancane, 17°05′S, 65°40′W, 1250 m, 3 Sep 2000, *M. Lehnert 54* (GOET, LPB, UC), ibid., *M. Lehnert 55* (GOET, LPB, UC); Chapare, Villa Tunari, terreno de "El Puente", 16°59′S, 65°35′W, 400 m, 12 May 1993, *P. Ibisch 93.0236* (LPB). **La Paz:** Abel Iturralde, Cantón San José de Chupiamonas, Serranía de Eslabon, 14°15′S, 68°04′W, 620 m, 18 Apr 1997, *St.G. Beck 24044* (LPB); Caranavi, Serranía Bella Vista, 46 km de Caranavi hacia Sapecho, 15°39′S, 67°28′W, 1200 m, 30 Aug 1997, *M. Kessler, J. Gonzales, & K. Bach 11625* (LPB, UC); Serrania Bella Vista, entre Caranavi y Palos Blancos, ca. km 48.8, 15°40′S, 67°24′W, 1200 m, 13 Aug 2000, *M. Lehnert 24* (GOET, LPB, UC); Sur Yungas, Serrania de Marimonos, Colonia San Martín "Agua Rica", 15°30′S, 67°20′W, 830 m, 01 May 1991, *R. Seidel 5096* (LPB); Larecaja, Mapiri, 15°19′S, 68°12′W, 500 m, 15 Sep 2001, *R.S. Williams 1272* (GH, LPB, NY, US). **Santa Cruz:** Ichilo, Parque Nacional Amboró, trail to campamento Mataracú from crossing over the Río Yapacani, 17°32′S, 63°52′W, 350 m, 1 Jun 1998, *M. Nee & L. Bohs 49575* (NY, UC); Ichilo, Parque Nacional Amboro, Campamento Mataracu, trails along river heading west, 17°34′S, 63°52′W, 430 m, 13 Aug 2003, *M.A. Sundue & M. Mendoza 896* (NY, UC).

Today the type locality Alto del Trigo is covered only in pastures and secondary vegetation, and *Cyathea lindigii* was not found there anymore despite a prolonged search in 2016. As currently defined, the species occupies two separate geographical and elevation ranges in the northern and central Andes, respectively, with no transition in Ecuador.

In both populations, plants may occur that have white scale margins in the central and upper petiole parts. These plants approach *C. acutidens* and *C.*

leucolepismata, which are easily distinguished by the presence of abundant hairs on the petioles, most of the leaf axes and veins; *Cyathea lindigii* lacks hairs on the petiole and is only sparsely hairy on the leaf axes and veins abaxially. *Cyathea lindigii* further lacks darker teeth or larger cell groups in the paler margins; these characterize at least the more bicolorous scales of *C. leucolepismata* (Fig. 3H, J)

Cyathea lindigii differs from *C. multiflora sensu stricto* in reaching larger dimensions (trunks to 10 m tall, leaves usually 2–4 m long vs. trunks to 4–5 m tall, leaves less than 2 m long in *C. multiflora*) and in the white margined petiole scales (vs. petiole scales with brown to yellowish margins).

Compared to *C. leucolepismata*, *C. lindigii* is most easily described as a glabrous variety of that species with darker petiole scales. In *C. lindigii*, the pinnules are completely glabrous except for some multicellular hairs on the costules and midveins adaxially; they may be, however, densely covered with unicellular trichomidia on and between the veins abaxially. *Cyathea leucolepismata* has many long, stout hairs similarly distributed abaxially. Varieties of *C. leucolepismata* with less hair than normal may be almost glabrous on the veins but are still densely hairy on the costules abaxially. In rare cases, *C. lindigii* may have some hairs on the costules abaxially, too (*e.g.*, *Kessler 11076*), but then the hairs are still scarcer, thinner, and more flaccid than in *C. leucolepismata*. These plants also have almost concolorous brown petiole scales, making it easier to distinguish them from *C. leucolepismata*, which has strongly bicolorous scales with wide whitish margins on trunk and petiole bases, but almost entirely whitish ones elsewhere on the petiole; most specimens of *C. leucolepismata* have only the whitish scales preserved.

6. ***Cyathea mariposana*** A.Tejedor & Lehnert, ***sp. nov.*** Type.—PANAMA. Veraguas: Cerro Mariposa, near Santa Fé, 08.497 N, 81.117 W, 1300 m, 08 Jan 2016, *M. Lehnert 3523 with A. Tejedor* (holotype: PMA!; isotypes: BONN!, Z!). **Figs. 10, 11A–D.**

Diagnosis.—Cyathea mariposana is a small, trunkless species with conspicuously glossy leaves above and with clearly visible venation below, similar in general leaf architecture to *Cyathea squamulosa*, differing from this species in the long lanceolate, apically twisted, and nearly concolorous petiole scales (vs. scales lanceolate, apically flat, and discordantly bicolorous with brown centers and light brown to beige margins in *C. squamulosa*).

Trunks absent, rhizome elevates apex just above substrate, trunk apex 6–7 cm diam, without old petiole bases; apices protruding above petiole bases. *Leaves* ca. 180 cm long, erect to distally arching. *Petioles* to 85 cm long, inermous to weakly and sparsely verrucate, lustrous green in live plants, glabrescent with flaccid hyaline multicellular hairs 1–2 mm long, scurf sparse, consisting of pale appressed ovate squamules to 0.5 mm long, and brown to dark brown ovate erect squamules to 1 mm long; petioles with conspicuous yellowish pneumathodes to ca. 2.0 × 0.5 mm. *Petiole scales* lanceolate, 15–20 × 2.5–3.5 mm, weakly concordantly bicolorous, shiny dark brown with narrow

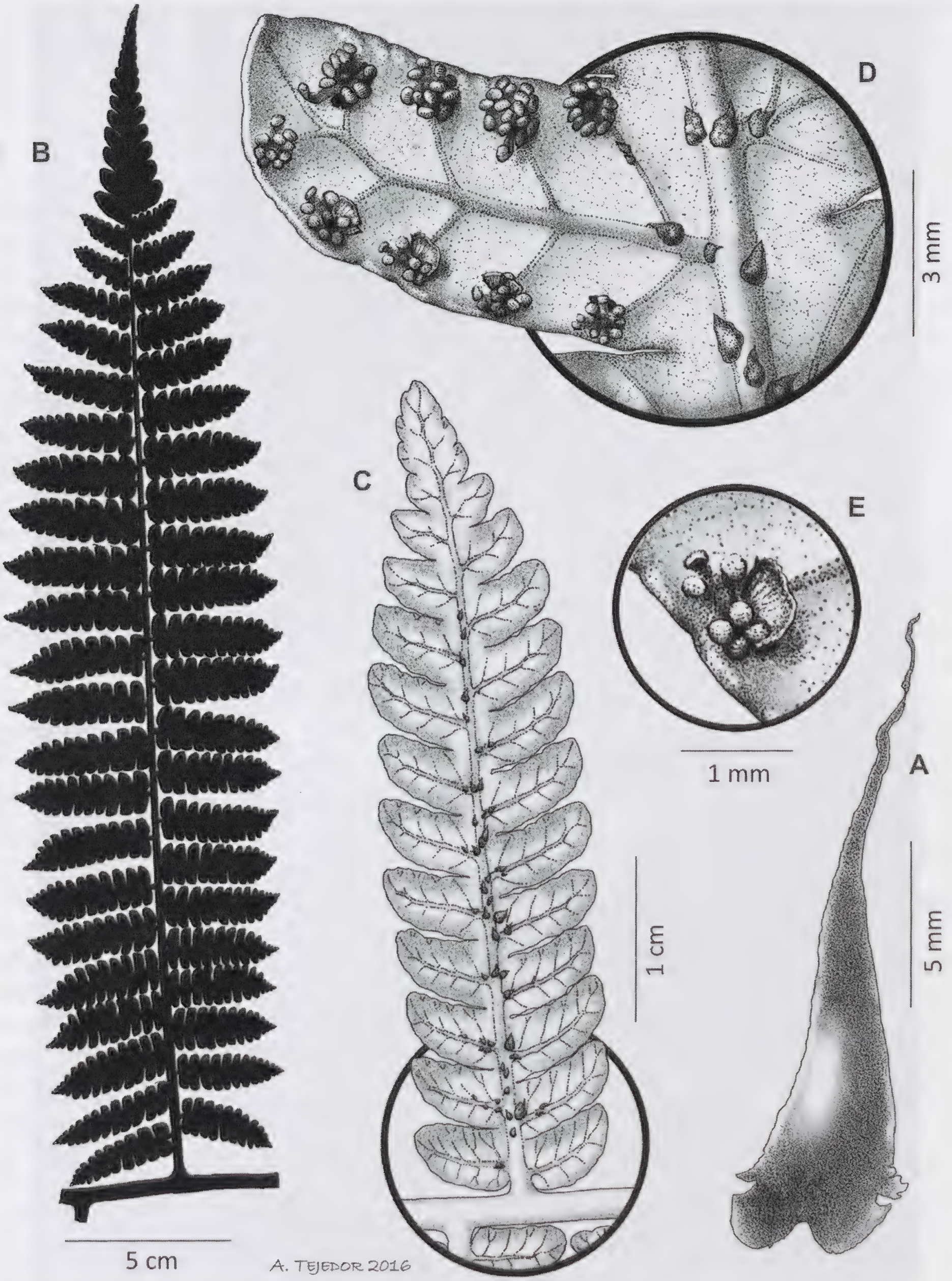

FIG. 10. *Cyathea mariposana*: A. Petiole scale. B. Pinna, silhouette. C. Pinnule, abaxially. D. Fertile segment, abaxially. E. Detail of sorus with hemitelioid indusium (All drawn from *M. Lehnert 3523 with A.Tejedor*, isotype BONN).

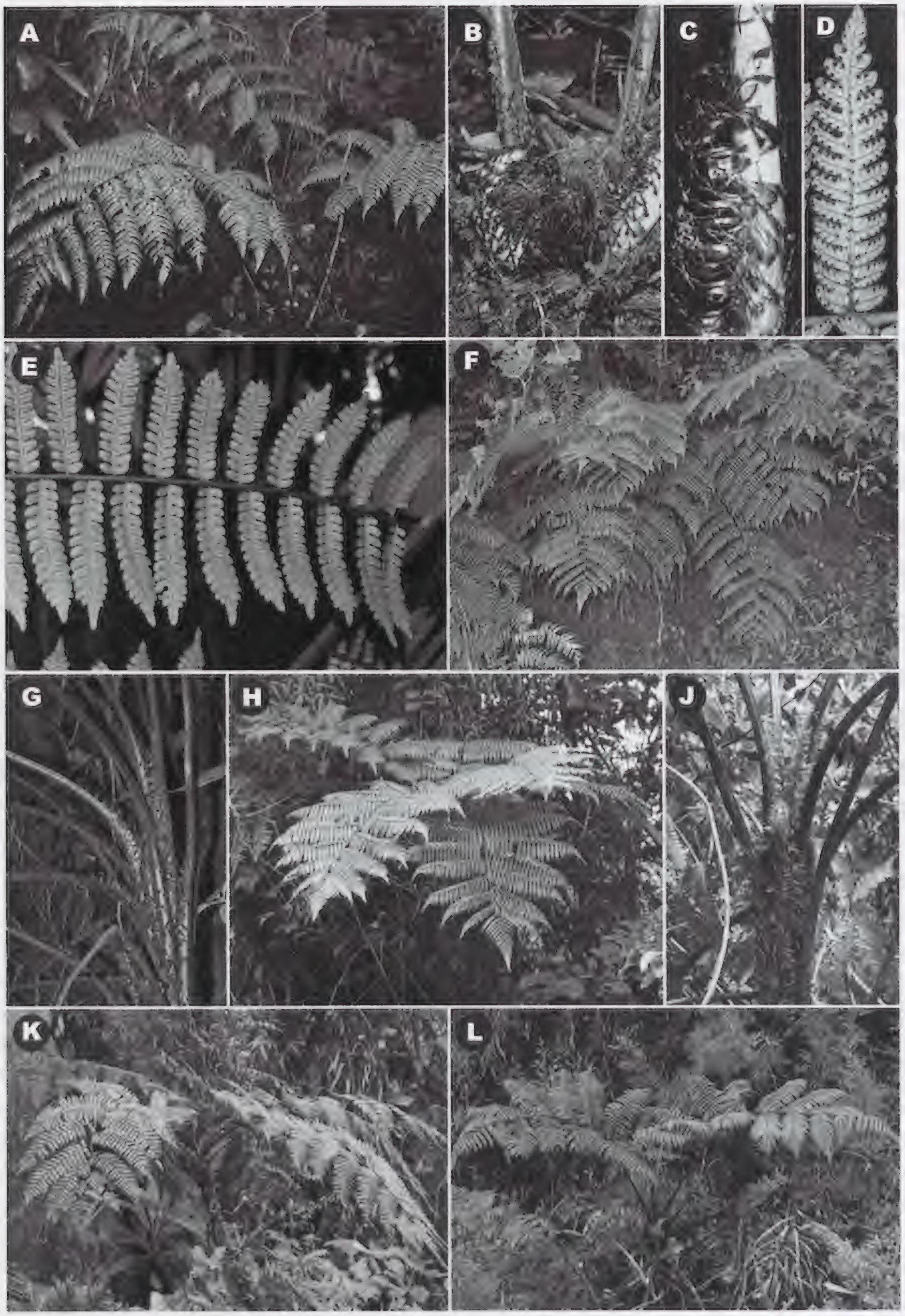

FIG. 11. Field characters. A–D. *Cyathea mariposana* (Veraguas, Panamá; photo of the type, A. Tejedor): A. Habit. B. Trunk apex. C. Petiole with scales. D. Fertile pinnules abaxially, showing submarginal sori. E–G. *Cyathea multiflora* (Veraguas, Panamá; *M. Lehnert 3506*, photos M. Lehnert): E. Pinnules abaxially. F. Crown. G. Upper trunk with petioles. H–J. *Cyathea paisa* (Antioquia, Colombia, *M. Lehnert 3001*, photos M. Lehnert): H. Crown. J. Upper trunk with petioles. K. *Cyathea retanae* (Darién, Panamá; photo, A. Tejedor). L. *Cyathea rojasiana* (Chiriquí, Panamá; photo A. Tejedor).

whitish margins near the base, scale tips concolorous dark brown; petiole bases cordate, often separated from rest of petiole by narrow constriction; apices attenuate, flat to weakly twisted; the differentiated margins narrow, without setae or teeth, usually long persisting. *Laminae* ca. 95 × 75 cm, broadly ovate, bipinnate-pinnatifid, firm herbaceous to chartaceous, lustrous dark-green adaxially, lustrous light green abaxially; apices rather abruptly reduced. *Rachises* inermous, lustrous yellowish green, dull brown in dry material. Largest *pinnae* ca. 30 cm long, pinnae subsessile to stalked to 1.3 cm, 7–9 pairs per leaf, alternate, patent to weakly ascending; inarticulate, distal segments simply adnate before ending in a pinnatifid apical section; basal pinna pairs slightly reflexed, ca. 3/4 the length of longest pinnae. *Costae* to 2 mm wide, inermous, yellowish brown abaxially, pale green adaxially; with green wings for most of its length but these upturned and thus inconspicuous; adaxially with many tan to brown, antrorsely curved, multicellular hairs to 1.0 mm, glabrous to glabrescent abaxially. Largest *pinnules* 50 × 15 mm, subsessile with stalks to 1.5 mm long, inarticulate, 1.2–1.4 cm between the costules, oblong, apically acuminate with lobed margins; costules olive green adaxially, bright green abaxially, hairy adaxially with tan to brown multicellular hairs 1.0 mm long, abaxially strongly prominent, glabrous to glabrescent with sparse thin erect hairs 1.0–1.5 mm long, with scattered ovate, dark brown subbullate scales, ca. 1.0–1.5 × 0.5 mm. *Costules* green, glabrous, basally without pneumathodes. Largest *segments* 7.0–8.0 × 2.5–3.0 mm, segments sessile, adnate, rarely remote proximally and then connected with laminar tissue, patent to weakly ascending, tips obtuse proximally to acute and slightly falcate distally; proximal segments subopposite, alternate through most of pinnule length; sinuses acute, < 1 mm wide; margins crenulate to subentire; veins planar or weakly protruding adaxially, darker than laminar tissue; adaxially with some multicellular hairs on the midveins and lateral veins, to 1 mm long, abaxially glabrous with subbullate to bullate dark brown squamules 1.0–0.5 × 0.5 mm with acute to subulate tips; fertile and sterile veins generally simple, rarely forked. *Sori* ca. 0.8–1.0 mm diam., submarginal, indusium hemitelioid, appressed, small, with erose margins, dark brown, hidden by sporangia; receptacles globose to columnar, 0.15–0.2 mm diam., paraphyses few, dark, shorter than sporangia (0.1–0.2 mm long), clustered at receptacle tips. Spores not examined.

Etymology.—The name refers to Cerro Mariposa (occasionally confused in the botanical literature with neighboring deforested Cerro Tute), the only known locality of the species and type locality of another three tree fern taxa.

Distribution and Habitat.—Only known from the type locality (Fig. 2C).

Cyathea mariposana was found in numbers in the understory of low canopy montane forest with soil covered in thick leaf litter and bryophytes, at a relatively narrow elevation band (1300–1350 m) below the windswept summit of Cerro Mariposa. Its trunkless habit may be an adaptation to a relatively well lit, yet regularly wet and mossy habitat.

Cyathea mariposana differs from *C. squamulosa* in the absence of a trunk (Fig. 11A) and the nearly inermous, basally patent petioles that expose the rhizome apex (vs. trunk to 2 m and petioles weakly aculeate to strongly verrucate, erect, obscuring growing apex in *C. squamulosa*). *Cyathea mariposana* could further be confused with small, trunkless individuals of *C. nigripes* (C.Chr.) Domin, sharing with this species a protruding apex, shiny dark scales, rather abruptly reduced leaf apex, and a lustrous dark green lamina; *Cyathea nigripes* can be distinguished by the dark brown to atropurpureous, aculeate petioles with whitish scurf (vs. petioles bright green, without scurf, and inermous to weakly verrucate in *C. mariposa*) and lack of indusia (vs. indusia small but present, hemitelioid).

Cyathea mariposana also resembles *C. retanae* from the Darién region (border Panamá and Colombia), as both species have submarginal sori, mostly simple unbranched fertile veins and notably cordate pinnule bases. *Cyathea retanae* is the larger one of the two species, developing a proper trunk, and it has larger, more hood-like hemitelioid indusia and more variation in petiole scale color, with some having much paler margins than those of *C. mariposa*, which are always concolorous brown.

7. *Cyathea multiflora* Sm., Mém. Acad. Roy. Sci. (Turin) 5. 416. 1793. *Hemitelia multiflora* (Sm.) R.Br. ex Spreng., Syst. Veg. 4(1): 126. [Jan–Jun] 1827. *Hemitelia multiflora* (Sm.) Desv., Mém. Soc. Linn. Paris 6: 321. [Jul–Sep] 1827, *nom. illeg. Alsophila multiflora* (Sm.) C.Presl, Tent. Pterid. 61. 1836. *Amphicosmia multiflora* (Sm.) Gardner, London J. Bot. 1: 441. 1842. Type.—"Amer. Merid.," *R. Shakespeare s.n.* (holotype: BM-000586111 [Herb. Banks]!, isotypes: LINN-HS1637-32 [image!], US [fragment of BM, image!]). — Provenance uncertain, see Maxon (1911) for comments. **Figs. 1F,G, 11E–G, 12, 13.**

Hemitelia denticulata Hook., Syn. Fil. (Hooker & Baker): 31. 1865. Type.—PITCAIRN ISLANDS (?). "Elizabeth Island" (= Henderson Island), *H. Cuming 1360* (holotype: K-000589973!/-000589974!).— Provenance dubious, see Lehnert (2011) for comments.

Hemitelia hartii Baker, J. Bot. 24: 243. 1886. *Cyathea hartii* (Baker) Domin, Pteridophyta 264. 1929. Type.—PANAMA. Bocas del Toro: Chiriqui Lagoon and its neighborhood, [ca. 0–50 m], Nov–Dec 1885, *J.H. Hart 43* (holotype: K-000589970!/-000589972!; isotypes: GH [photo US] n.v., NY-00148969 [image!], P-00625700 [image!], US-00066089 [image seen]).

Alsophila decussata Christ, Prim. Fl. Costaric. 3: 41. 1901. *Cyathea decussata* (Christ) Domin, Pteridophyta: 264. 1929. Type.—COSTA RICA. Puntarenas: Vallé de Diquis, [ca. 08°52′58″N, 83°29′42″W] 700 m, 06 Feb 1886, *H. Pittier 12027* (holotype: P-00625695 [image seen]; isotypes: BR-0000006978525 [image seen], F-0075868F [fragment], NY-00148658 [image seen], P-00625693 [image seen]/-00625694 [image seen], UC-1550956!, US-00066081[image seen]).

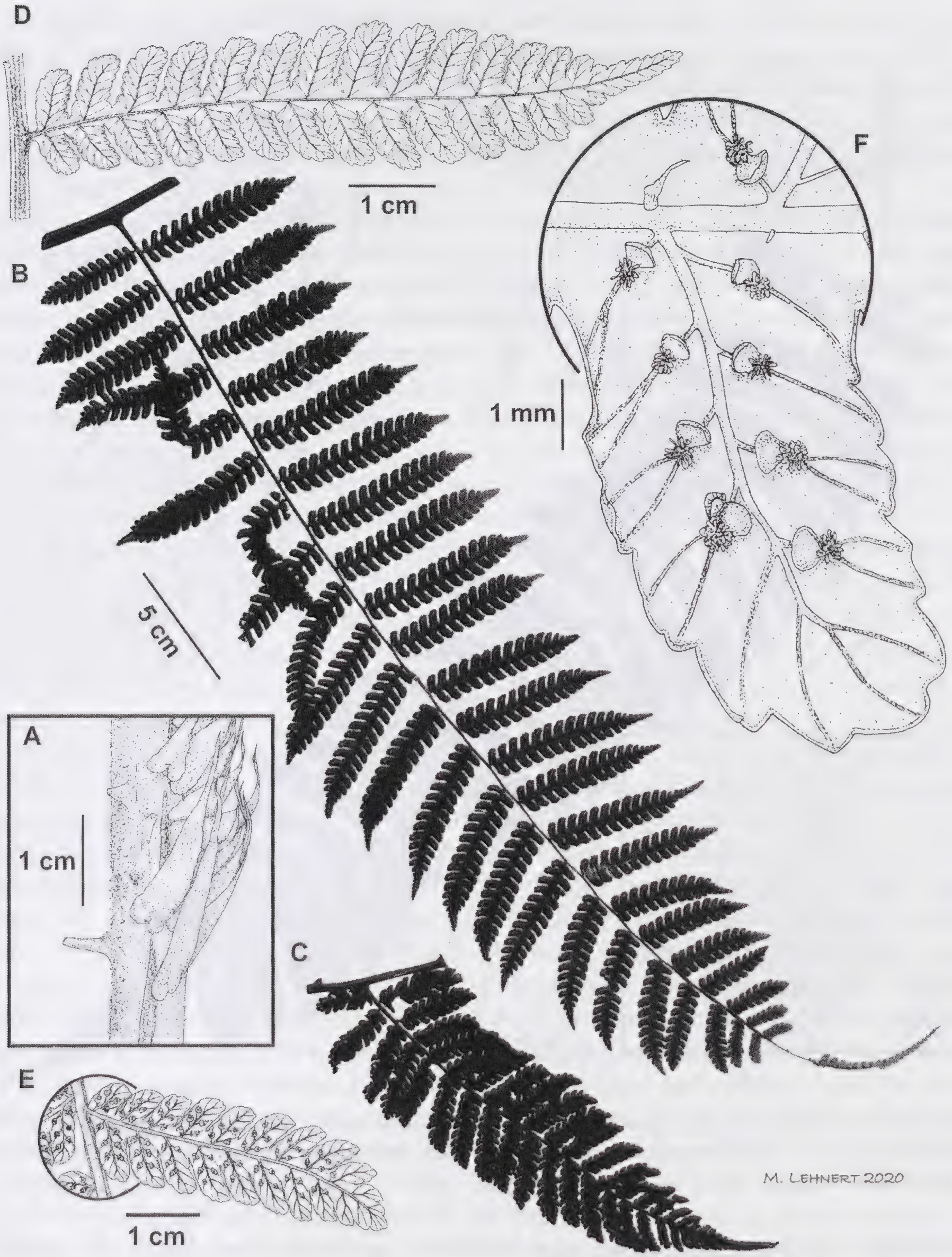

FIG. 12. *Cyathea multiflora*: A. Petiole with scales. B–C. Medial pinnae, silhouette. D. Pinnule, adaxially. E. Pinnule, abaxially, fertile. F. Segment, fertile, abaxially. A, B, D, F drawn from *M. Lehnert 3506 with A. Tejedor* (BONN); C, E drawn from *R. Shakespeare s.n.* (holotype BM).

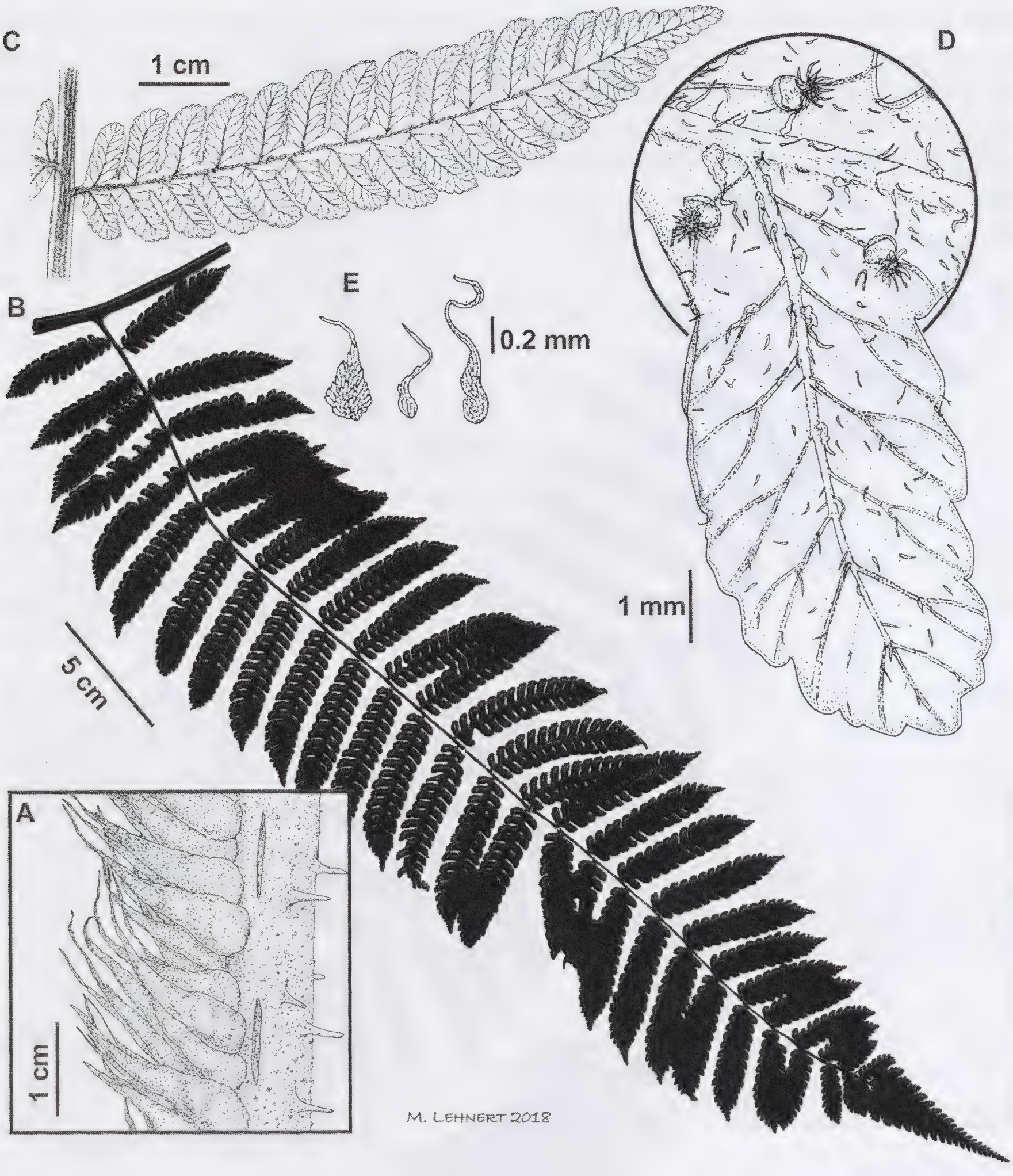

FIG. 13. *Cyathea multiflora* (type "*hartii*"): A. Petiole with scales. B. Medial pinna, silhouette. C. Pinnule, adaxially. D. Segment, fertile, abaxially. All drawn from *Lehnert 3497 with A. Tejedor* (BONN).

Trunks 1.5–3.0 m tall, erect to decumbent, 4–10 cm diam., with old petiole bases; apices hidden between petiole bases; without adventitious buds. *Leaves* 125–150 cm long, stiffly erect to distally arching. *Petioles* 35–70 cm long, sparsely to strongly aculeate with prickles to 5 mm long, dark stramineous to blackish brown, matte, glabrous or glabrescent with dense scurf consisting of appressed trichomidia and branched hairs to 0.5 mm long, rarely basally with some small erect reddish brown squamules with crested margins; petioles on each side with a discontinuous line of pneumathodes to 7 × 1.5 mm, pale brown. *Petiole scales* ovate-lanceolate to lanceolate, to 15.0–25.0 × 3.5–5.0

mm, mostly concordantly bicolorous, shiny dark brown to dark castaneous with golden brown to yellow margins, in upper petiole parts becoming paler to almost concolorous reddish brown, but never whitish or matte; bases cordate to rarely peltate, apices long acute, flat to weakly twisted; the differentiated margins narrow, finely serrate, without setae or teeth, usually long persisting. *Laminae* to 120 × 70–90 cm, ovate-elliptic, bipinnate-pinnatifid, firm herbaceous to chartaceous, dark-green adaxially, often blackish when dried, gray-green abaxially; apices gradually reduced. Rachises inermous or in larger plants basally aculeate with prickles to 4 mm long, yellowish brown to dark brown abaxially and adaxially; with multicellular hairs to 0.5–0.8 mm long on both sides, tan to brown and dense adaxially, white, hyaline, and rather sparse abaxially. Largest *pinnae* 35–50 cm long, pinnae short-stalked 0.5–1.5 cm, 11–15 pairs per leaf, alternate, weakly to strongly ascending; inarticulate, distally narrowly to broadly green-alate, distal segments simply adnate before ending in a pinnatifid apical section; basal pinna pairs reflexed, ca. 2/3 the length of longest pinnae. *Costae* 1.5–2.0 mm wide, inermous, dark stramineous to grayish brown abaxially, dark grayish brown adaxially; adaxially with many tan to brown, antrorsely curved, multicellular hairs to 1.0 mm, abaxially with very thin appressed to ascending hairs to 0.5 mm long; junctures of costae and rachises weakly swollen abaxially, each bearing a planar elliptic pneumathode to 1.0–3.0 × 1.0–1.5 mm, orange-brown, sometimes blackened, inconspicuous. Largest *pinnules* 65–90 × 15–19 mm, subsessile, stalked to 1–2 mm, inarticulate, 1.3–1.8 cm between the stalks/costules, oblong to oblanceolate, weakly cordate to weakly cuneate basally; pinnules acute to short-attenuate apically with serrate margins. *Costules* yellowish brown to dark brown or blackish adaxially and abaxially, weakly to strongly prominent and densely hairy adaxially with tan to brown multicellular hairs to 0.5(-1.0) mm long, abaxially planar or weakly prominent, moderately to densely hairy with thin hairs erect 0.5-0.8 mm long and some lanceolate, orange-brown scales, flat ones to 2.0 × 0.5 mm, bullate ones usually only half the size; costules basally without pneumathodes, green alate and continuous with costae, or set against the costae with a black line abaxially in dried specimens. *Segments* 8.0–10.0 × 3.0-4.0 mm, sessile, adnate, rarely remote and then connected with laminar tissue, ascending, distally falcate, tips obtuse to rounded; proximal segments alternate to subopposite, usually smaller or as long as following segments; sinuses acute, to 1.0–2.0 mm wide; margins serrate (each vein ends in a separate marginal lobe), not different in proximal segments; veins planar or weakly protruding on both sides, in the color of the laminar tissue or yellowish to brown; veins adaxially with some multicellular hairs on the midveins and few on the lateral veins, abaxially usually without hairs, also between the veins; sterile veins simple, fertile veins simple or rarely forked. *Sori* ca 1.0 mm diam., medial to supramedial, on the back or in the fork of veins; indusia hemitelioid, reaching 1/4–1/3 around to the receptacles, glabrous, pale brown, matte, firm, ascending, hidden in intact sori, sometimes partly arching over receptacles when sporangia are shed, margins with shallow lobes, sometimes bivalved in over-mature sori; receptacles globose to columnar, 0.3-0.4 mm

diam., paraphyses few, often clustered at the top of the receptacles, tan to brown, somewhat flattened, of the same length or shorter than the sporangia (0.2–0.4 mm long). *Spores* not examined.

ETYMOLOGY.—The epithet refers to the sori, which historically sometimes had been referred to as either fructifications or inflorescences of ferns (Latin *multiflorus* = many flowered). This species does not have particularly abundant sori compared to other species of the genus, but on the small leaves of the type, the sori appear densely arranged.

DISTRIBUTION AND HABITAT.—Belize(?), Guatemala, Costa Rica, Panama (Fig. 2B) at 0–1450 m, and western Colombia (Alto del Buey, Chocó) at 1450–1750 m, in understory of rainforests, flourishing in semi-shade along trails and tree fall gaps.

ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. **Heredia:** P.N. Braulio Carillo, Reserva La Selva, near Puerto Viejo de Sarpiqui, 10°25.575′N, 84°00.756′W, 84 m, 15 Nov 2012, *M. Lehnert 2629* (BONN, INB). **Limón:** Cordillera de Talamanca, Cantón de Matina, 0.5 km aguas arriba de la desembocadura de la quebrada Cañabral en Río Barbilla, margen izquierda, 10°01′N, 83°25′W, 100–200 m, 29 Oct 1988, *G. Herrera 2247* (UC, MO). **Puntarenas**: Cantón de Coto Brus, Estación Biológica Las cruces, 08°47′10″N, 82°57′40″W 1100 m, 18 Jun 2002, *B. Boyle, R. Kirkpatrick, & S. Kuchel 6393* (UC); along road between Chacarita and Rincón de Osa, 10 km W of Chacarita, 08°45′N, 83°18′W, 100 m, 06 Mar 1985, *T.B. Croat & M.H. Grayum 59891* (UC); ridge between Río Convento and quebrada Segundo, ca. 1.5 km S of Carretera Interamericana, Valle de El General, 09°14′N, 83°30.5′W, 600 m, 10 Aug 1985, *M.H. Grayum & B. Hammel 5584* (UC); Osa Peninsular, 15 km S of Tropical Science Center field station and ca. 20 km S of Rincón de Osa, 150 m, 18 Jul 1967, *J.T. Mickel 2795* (UC); vicinity of Biological Field Station at Finca Wilson, 5 km S of San Vito de Java, 1100–1200 m, 02–06 Aug 1967, *J.T. Mickel 3179* (UC). **San José**: opposite of forest reserve of Ministerio de Agricultura, 20 km S of San Isidro del General, 645 m, 18 Jul 1963, *A. Jimenez 872* (UC); 25 km S of Villa Millson the way to San Isidro on the Interamerican Highway, 1450 m, 10 Aug 1967, *J.T. Mickel 3292* (UC).

PANAMA. **Chiriquí:** Fortuna Dam Project Area, ca. 8 km N of Main Camp, 08°41′N, 82°12′W, 1200-1400 m, 11 Nov 1980, *K.J. Sytsma & W.D. Stevens 2311* (UC) along road between Chiriquí Grande and Fortuna, 7.7 miles W of Chiriquí Grande, 1.5 miles W of Punta Peña, 08°50′N, 82°10′W, 80 m, 09 Mar 1985, *T.B. Croat & M.H. Grayum 60098* (UC, MO). **Coclé:** near La Mesa, 11 Feb 1971, *T.B. Croat 13348* (UC). **Panamá:** Distrito San Blas, 09°18.981′N, 79°00.372′W, 200 m, 11 Jan 2016, *M. Lehnert 3497 with A. Tejedor* (BONN, PMA); Sendero de interpretación, 150 m de la torre de comunicaciones del INTEL, con orientación suroeste en Dirección a Panamá, 800–900 m, 20 Apr 1994, *E. Morris 95* (COL, PMA); Cerro Campana, 08°40′N, 79°55′W, 700 m, 08 Sep 1982, *G. Hamilton, W. D'Arcy & D. Roudik 1163*(UC, MO); Cerro Campana, 500–1000 m, 14 Feb 1981, *W. D'Arcy & K. Sytsma 14641*(UC). **Veraguas:** Road San Felix -

Cerro Colorado, 08°23.765′N, 81°46.596′W, 550 m, 07 Jan 2016, *M. Lehnert 3506 with A. Tejedor* (BONN, PMA).

COLOMBIA. **Chocó:** NW side of Alto del Buey, trail along ridge from the confluence of the forks of the Río Mutatá, above Río Dos Bocas to the top of Alto del Buey, 1450–1750 m, 09 Feb 1971, *D.B. Lellinger & E.R. de la Sota 254* (COL, US).

Compared to the many species formerly united under this name, *Cyathea multiflora* has mid-sized pinnules with acute to short-attenuate tips and well-armed petioles that bear some evident squamellate scurf when young. It is not visibly hairy abaxially and squamules are never abundant.

The type of *C. multiflora* seems to lack squamules completely, but this may be due to the old age of the specimens; it lacks hairs abaxially, and is only sparsely hairy adaxially on the costules, with relatively strong brown hairs to 1 mm long. The indusia are rather large, brown, and the pinnules only up to 33 × 10 mm. In comparison, the types of the synonyms have more of the fine indument abaxially, but it is generally scant and inconspicuous. The type of *Hemitelia hartii* has well-developed indusia but its segments appear rather blunt, separated by relatively wide sinuses. The type of *Alsophila decussata* has comparatively small indusia and sharply serrate segment margins; it can be best described as a glabrous version of *C. pinnula*. The types of the four names here united display a gradual increase in pinna size (from *H. multiflora* over *A. decussata, H. hartii* to *H. denticulata*) which we interpret as natural amplitude of one adaptive species, although the two older names lack the crucial petiole with their distinctive scales in their type material. All these forms appear to agree in the fact that the lower pinnae are visibly stalked while those in the upper half of the leaf are sessile (although they still may be of the same length as the lower ones).

In Panama, besides the regular abaxially glabrous forms (which correspond in pinna outline with the synonym *Hemitelia hartii*), we collected at least one plant (Fig. 12) with abundant short hairs abaxially (Bocas del Toro, *M. Lehnert 3497 with A. Tejedor*; BONN, PMA). We first aligned it with the herein described *C. pinnuloides* but saw too much incongruence in general proportions of the leaf parts and color pattern of the scales. Further studies may focus on potential introgression between *C. multiflora* and the sympatric *C. pinnula*.

Most specimens still labelled as *Cyathea multiflora* from Mesoamerica north of Costa Rica can be attributed either to *C. austroamericana* (*i.e.*, specimens with small blunt tipped pinnules; Fig. 5) or *C. grayumii* (*i.e.*, specimens with larger acute tipped pinnules), which both have very dark brown to blackish petiole scales with thin whitish margins. However, a large proportion of these specimens has no petiole scales preserved and thus cannot be confidently addressed. Indeed, *C. austroamericana* is very similar to *C. multiflora* in size, proportions, and indument.

We had no confirmation for an occurrence of *Cyathea multiflora* north of Costa Rica, until we came across photographic evidence from Guatemala (Véliz Pérez & Vargas Ponce, 2006), where the species supposedly has a wider range.

During our revision we found one sterile collection from Belize (*C. Whitefoord 1795*; BM-000787539 [3 sheets]) matching *Cyathea multiflora* (as described here) in all vegetative characters. The fertile collection *Steyermark 39965* (US-01448969/-01448970 [image!]) may be a true *C. multiflora* from Guatemala, lacking petiole scales but annotated to be close to "no. 39963 [= *Cyathea schiedeana* (C.Presl) Domin], but [. . .] scales at base of stipe more rufous-brown and bark smoother with the leaf bases more prominent". Resolution of this species complex cannot be obtained without further field observations and the collection of more, complete specimens.

8. ***Cyathea paisa*** Lehnert, F.Giraldo & W.D.Rodr., **sp. nov.** Type.—COLOMBIA. Antioquia: between San Rafael and San Carlos, 06°17.201′N, 74°55.355′W, 1600 m, 21 Feb 2015, *M. Lehnert 3161 with M. Kessler, F. Giraldo & W.D. Rodríguez* (holotype: HUA!, isotypes: BONN!, Z!). **Figs. 1H, 11H–J, 14.**

Diagnosis.—Cyathea paisa has a unique combination of characters among the hemitelioid indusiate species of the genus, with overall small stature and trunks to 6 cm diam., petiole scales shiny orange-brown with paler golden brown to yellow margins, and short hairs on the lamina abaxially, differing in this regard especially from the sympatric *C. lindigii* (petiole scales auburn to dark brown, concordantly to discordantly bicolorous with narrow whitish margins, taller stature and trunks to 15 cm diam., lamina almost glabrous).

Trunks 1.0–3.5 m tall, erect, (2.5–)5–6 cm diam, with old petiole bases, these often rotting in lower parts, giving the trunk a stretched hourglass shape; apices hidden between petiole bases; without adventitious buds. *Leaves* 160–220 cm long, erect to distally arching. *Petioles* to 50 cm long, sparsely aculeate with prickles to 2 mm long, dark stramineous to blackish brown, matte, glabrescent with dense scurf consisting of appressed trichomidia and branched hairs to 0.5 mm long, rarely basally with some small erect pale brown squamules with crested margins; petioles with inconspicuous brown pneumathodes 11 × 1 mm. *Petiole scales* ovate-lanceolate to lanceolate, 15.0–25.0 × 2.0–3.5mm, weakly concordantly bicolorous, shiny orange-brown (rarely darker) with paler golden brown to yellow margins (in fresh material, generally paler when dried), in upper petiole parts not becoming paler, bases cordate to rarely peltate, apices attenuate, flat to weakly twisted; the differentiated margins narrow, finely serrate, without setae or teeth, usually long persisting. *Laminae* 170–200 × 70-100 cm, ovate-elliptic, bipinnate-pinnatifid, firm herbaceous to chartaceous, dark-green adaxially, often blackish when dried, gray-green abaxially; apices gradually reduced. *Rachises* inermous or with few small prickles to 1 mm long basally, yellowish brown to dark brown abaxially and adaxially; with multicellular hairs to 0.5-0.8 mm long on both sides, tan to brown and dense adaxially, white, hyaline, and rather sparse abaxially. Largest *pinnae* 35–50 cm long, pinnae short-stalked 0.5–1.5 cm, (7–)13–16(–20) pairs per leaf, alternate, patent to weakly ascending; inarticulate, distally narrowly to broadly green-alate, distal segments simply adnate before ending in a pinnatifid apical section; basal pinna pairs reflexed, ca. 2/3 the length of longest pinnae. *Costae* 1.5–2.0

mm wide, inermous, dark stramineous to grayish brown abaxially, dark grayish brown adaxially; adaxially with many tan to brown, antrorsely curved, multicellular hairs to 1.0 mm, abaxially with very thin appressed to ascending hairs to 0.5 mm long, also with remnants of brown scurf; junctures of costae and rachises weakly swollen abaxially, each bearing a planar elliptic pneumathode to 1.0–3.0 × 1.0–1.5 mm, orange-brown, sometimes blackened, inconspicuous. Largest *pinnules* 70–95(–140) × 15(–28) mm, subsessile, stalked to 1(–2) mm, inarticulate, 1.4-2.0 cm between the stalks/costules, oblong to oblanceolate weakly cordate to weakly cuneate basally; pinnules long acute to short-attenuate apically with serrate margins. *Costules* yellowish brown to dark brown or blackish adaxially and abaxially, weakly to strongly prominent and densely hairy adaxially with tan to brown multicellular hairs 1.0 mm long, abaxially planar or weakly prominent, moderately to densely hairy with white to tan, thin erect hairs 0.5-0.8 mm long, with few to many lanceolate, orange-brown scales, flat ones to 2.0 × 0.5 mm, bullate ones ca. 0.5–1.0 × 0.5 mm, slender, with subulate to filiform, often paler to white tips, in young leaves also with pale brown or bicolorus white/brown scurf remnants (tortuous, appressed branched hairs); costules basally without pneumathodes, set against the costae with a black line abaxially in dried specimen. Largest *segments* 8.0-11.0 × 3.0-4.0 mm, segments sessile, adnate, rarely remote and then connected with laminar tissue, ascending, distally falcate, tips obtuse to rounded; proximal segments alternate to subopposite, usually smaller as following segments; sinuses acute to obtuse, to 2.0 mm wide; margins serrate (each vein ends in a separate marginal lobe), not different in proximal segments; veins planar or weakly protruding on both sides, in the color of the laminar tissue or yellowish to brown; adaxially with some multicellular hairs on the midveins and few on the lateral veins, to 0.5(–1.0) mm long, abaxially with bullate squamules and scurf remnants on midveins, with few to many erect, tan to white multicellular hairs to 0.5 mm long, also between the veins, in young leaves also along the margins; sterile veins simple or forked, fertile veins forked. *Sori* 0.7–0.9 mm diam., medial to supramedial (appearing submarginal if segments margins are revolute), in the fork of veins; indusia hemitelioid, reaching 1/4–1/3 around to the receptacles, glabrous, pale brown, opaque, firm, ascending, not arching over sori, margins with shallow lobes; receptacles globose to columnar, 0.2-0.3 mm diam., paraphyses few to many, often clustered at the top of the receptacles, tan to brown, weakly complanate, of the same length or shorter than the sporangia (0.2-0.4 mm long). *Spores* not examined.

ETYMOLOGY.—"Paisa" is a Colombian name for person originating from the Dept. Antioquia, often used in the sense of "commoner" or "fellow". We find the name appropriate because the species can be seen often along roads through forests in Dept. Antioquia. The name a noun in apposition.

DISTRIBUTION AND HABITAT.—Northern and central Colombia (Antioquia, Caldas, Cordoba, Tolima), mainly on the flanks of the Magdalena valley (Fig. 2C), in wet lower montane forests at 50–1700(–2000) m.

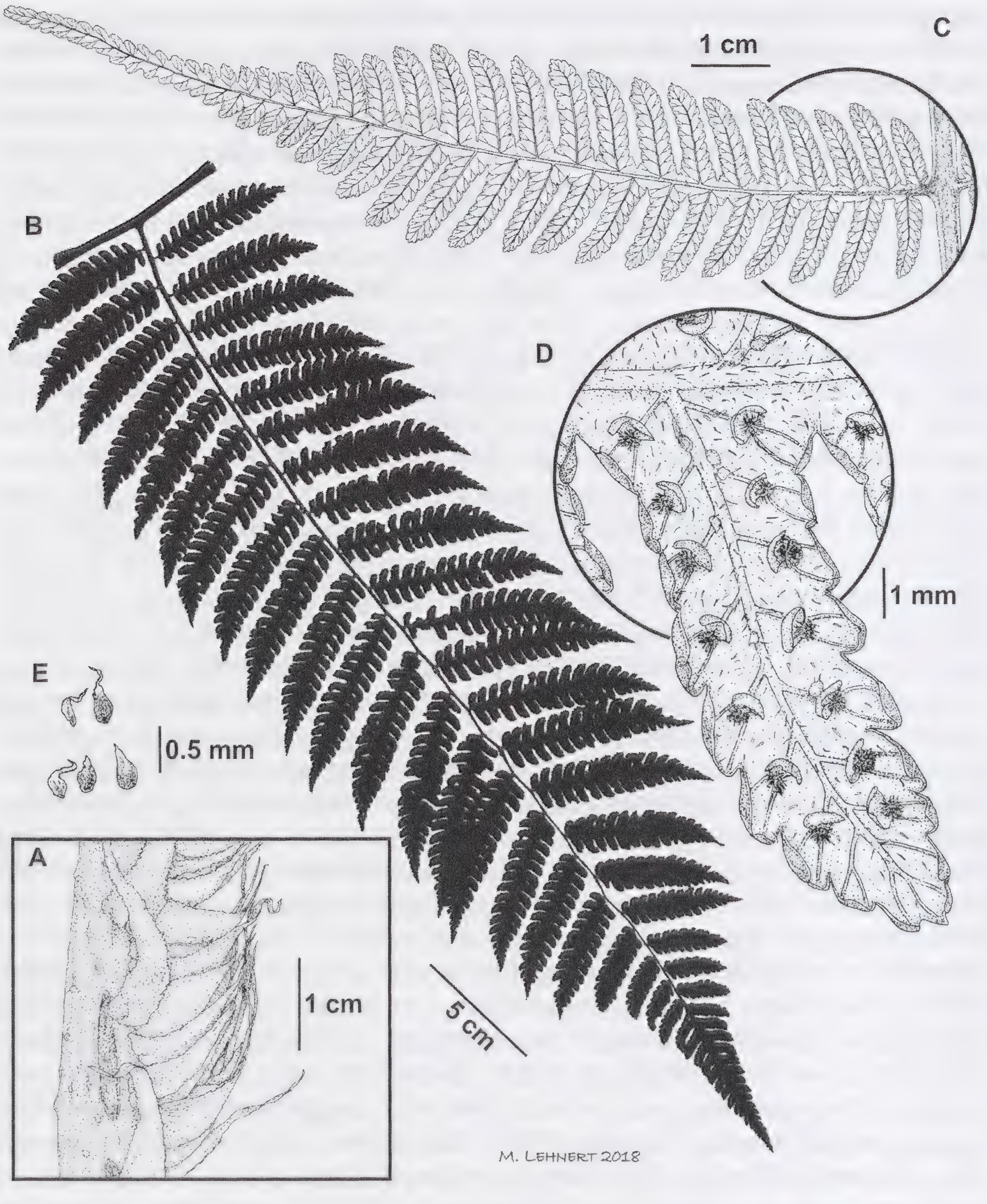

FIG. 14. *Cyathea paisa*: A. Petiole with scales. B. Medial pinna, silhouette. C. Pinnule, adaxially. D. Segment, fertile, abaxially. E. Squamules from costa. (All drawn from *M. Lehnert 3022*, paratype BONN)

ADDITIONAL SPECIMENS EXAMINED (PARATYPES).—COLOMBIA. **Antioquia:** Santo Domingo, Corregimiento Porce, 5 km de Porcecito finca de Fdo Vargas, 06°33′06.01″N, 75°12′56.8″W, 1000–1100 m, *L. Albert 81* (HUA); Tarazá, Corregimiento el doce, Vía a Barro Blanco, 1 km al este, Quebrada Puquí, Finca

Corrales, 07°28′22.9″N, 75°15′10.43″W, 260–280 m, *A. Arbeláez 218* (HUA); Puerto Berrio, Montes de la Carlota, 06°29′28.85″N, 74°33′21.2″W, 500–580 m, *L. Atehortúa 89* (HUA); Finca El Darién, 07°14′58″N, 76°25′55″W, 200 m, *L. Atehortúa 147* (HUA); Reserva Forestal del municipio Mutatá, frente al palacio municipal, 07°32′58″N, 76°25′56″W, 1150 m, *R. Callejas 2387* (HUA, NY); *ibid.*, *R. Callejas 2388* (HUA, NY); Remedios, vereda Santa Lucia, entre 9 y 18 Km al SO de Remedios en la vía Puerto Berrío, 06°34′50.43″N, 74°35′18.44″W, 530–640 m, *R. Callejas. 8081* (HUA); ibid., Corregimiento de Santa Isabel, entre 20 y 30 Km de Remedios, en la vía Puerto Berrio, 74°40′26.37″W, 06°58′36.27″N, 600–660 m, *R. Callejas 8109* (HUA); Barbosa, Km 42, vía Medellín-Porce, Parcelación Estación Popalito, 06°28′23.28″N, 75°16′19.03″W, 1000–1320 m, *R. Callejas 13314* (HUA); Corregimiento Santiago, 75°08′22.8″W, 06°32′57.4″N, 1650 m, *A. Camargo 876* (HUA); Caracolí, Vereda La Mesa, finca La Victoria, sector Colombia, 06°15′20.19″N, 74°38′42.97″W, 325–350 m, *J. Castro 625* (HUA); Cañon del Río Claro, sector NO, 05°53′N, 74°39′W, 170 m, *A. Cogollo1736* (HUA, JAUM, MO); San Rafael, Vereda El Bizcocho, quebrada La Cazuela, 06°18′15″N, 75°04′20″W, 1100 m, *J. Colorado 97* (HUA); Guatapé, Vereda Santa Rita, finca Montepinar, 06°28′N, 75°20′W, 1850 m, *N. Contreras 200* (HUA); San Carlos, Vereda Patio Bonito, Alto El Cerrón. 06°15′N, 75°10′W, 1100 m, *E. Correa 132* (HUA); Yolombó, Finca La Calandría, area de influencia de PORCE II, 06°36′46.19″N, 75°08′35.88″W, 985–1100 m, *H. David 896* (HUA); Vía Juanes - El Jordán, 06°15′10″N, 74°52′19″W, 800 m, *H. David 3341* (HUA); Anori, Planta Providencia, a 26 Km S y a 23 Km O de Zaragoza, en el valle del Río Anorí, entre Dos Bocas y Anorí, 07°19′05.83″N, 75°03′25.45″W, 400–450 m, *J. Denslow118* (HUA,MO); Anori, Vereda El Roble, 06°58′01″N, 75°8′29″W, 1300 m, *O. Díaz 715* (HUA); Santiago, Corregimiento de Santiago, Sector La Negra, a 9 Km de Santiago, 07°14′49″N, 75°10′00″W, 150–200 m, *R. Fonnegra 1972* (HUA); Cocorná, Vereda La Piñuela, Carretera a San Francisco, 06°01′29.86″N, 75°08′17.38″W, 700–980 m, *D. Giraldo, 489* (HUA); Porce, Cerca de la Qda. La Guinea, 07°13′00″N, 75°02′60″W, 975 m, *F. Giraldo 2048* (HUA, JAUM); Anori, Vereda Madre seca, finca de Fernando Muñoz, 670 m, *F. Giraldo 2540* (COL, JAUM); Anori, 07°15′06.66″N, 75°02′09.8″W, 670 m, *F. Giraldo 2549* (HUA, JAUM); Anori, Vda Madre seca, carretera cerca del poblado, 07°17′N, 75°02′W, 700 m, *F. Giraldo 2555* (COL, HUA, JAUM); Cáceres, Vereda Anará, finca La Magdalena, propietario Nivardo Zapata, 05°57′02″N, 74°52′11″W, 285 m, *F. Giraldo 2616* (HUA); Vereda La Josefina, al borde de la vía Medellín-Bogotá, Quebrada La Cristalina', 06°17′02.01″N, 74°55′03.55″W, 400 m, *F. Giraldo 2813* (HUA); Vereda Alta Vista, 07°14′02.39″N, 75°02′6.48″W, 700–800 m, *A. Gomez 1* (COL); Valle del Río Medellín, Porce, 1100 m, *W.H. Hodge 6872* (COL); San Luis, 800 m, *S. Hoyos 305* (JAUM); Anori, between Anori and Yarumal, 07°02′01.47″N, 75°10′15.1″W, 850–980 m, *M. Lehnert 3001* (BONN, HUA, Z); Corregimiento La Piñuela, quebrada "La Granja", 06°00′40.6″N, 75°05′01.49″W, 740–780 m, *M. Lehnert 3022* (BONN, HUA, Z); 4.8 Km al E of San Rafael, 06°16′N, 75°02′W, 1040 m, *J. Luteyn 11745* (HUA, NY); San Rafael, Vda. EL Charco, 1010–1200 m, *J. A. Montes 369* (HUA); San Roque, Vereda Monjas, 06°30′17.159″N,

74°55′42.88″W, 1340 m, *D. Montoya 148* (HUA); Granada, Vda. La Gaviota, Fca. De Luís Pinche, 06°06′15.93″N, 75°04′35.97″W, 1200 m, *M. Montoya 853* (HUA); Maceo, Vereda San Pedro, Finca San Pedro, 06°24′13″N, 74°45′38″W, 970 m, *P. Morales 311* (HUA); Vereda Santa Bárbara, 06°32′04.62″N, 74°30′17″W, 300–405 m, *A. Patiño 50* (HUA); Briceño, Vereda Palestina, 07°07′04.38″N, 75°31′50.92″W, 790 m, *C. Quijano 65* (HUA); San Luis, Quebrada la Cristalina, 06°32′58″N, 75°10′00″W, 550–750 m, *J. Ramirez 561* (COL, JAUM), ibid., 550–750 m, *J. Ramirez 1113* (COL, JAUM), *ibid.*, 550–770 m, *J. Ramírez 1130* (COL, MO); Pto Nare, Vda. Los Limones, 06°10′19.68″N, 74°46′56.82″W, 650 m, *J.F. Restepo, 246* (HUA); Nechí, Vereda Santa María, cerca de la capilla, al borde de la quebrada Santa María, 07°15′06″N, 75°02′09″W, 600 m, *W.D. Rodríguez 6567* (COL, MEDEL); Vereda Buenos Aires, cercanía del Río Alicante, borde de carretera, 06°34′09.81″N, 74°32′08.55″W, 400–500 m, *D. Tuberquia 2562* (HUA); Santo Domingo, 06°00′55.2″N, 74°57′56.04″W, 1200 m, *R. Scolnik 5291* (MEDEL); Anori, Planta Providencia, 26 kilómetros al sur y 23 kilómetros al occidente por aire de Zaragoza, en el valle del río Anorí entre Dos Bocas y Anorí, 07°19′5.83″N, 75°03′25.45″W, 400–700 m, *J.D. Shepherd 349* (COL, HUA), Anori, Corregimiento de Providencia, vicinity of the hydroelectric plant, 07°20′40.42″N, 75°02′02.24″W, 500–600 m, *D. Soejarto 2673* (HUA), Anori., Corregimiento Providencia, 500–600 m, *D. Soejarto 2900* (COL); Anori, Buenos Aires, 500–600 m, *D. Soejarto 3208* (COL, MO); Anori, entre la Tirana y Ajibe, 500–700 m, *D. Soejarto 3262* (COL); Segovia, Corregimiento La Fragua, Machuca, sitio Quintanilla, 07°18′9.48″N, 74°49′53.72″W, 254 m, *P. Trujillo-Q. 5338* (HUA); Vegachí, Paso Real, 06°58′40″N, 74°43′17″W, 890 m, *P. Trujillo-Q. 5748* (HUA), ibid., *P. Trujillo-Q. 5749* (HUA); 1.3 Km aguas abajo del puente, sobre el Río Samaná, márgen izquierda, 06°00′39.07″N, 74°56′15.52″W, 500 m, *P. Trujillo-Q. 6229* (HUA); Argelia, 05°38′39.25″N, 75°07′16.49″W, 945 m, *P. Trujillo-Q. 7706* (HUA); Vereda Tres Piedras, 06°32′59.53″N, 74°47′39.56″W, 700–900 m, *W. Uribe 101* (HUA); Vereda El Topacio, 06°30′32.85″N, 74°56′27.91″W, 950 m, *C. Velásquez 6872* (HUA). **Caldas:** Norcasia, Vereda La Quiebra de Roque, Reserva Río Manso, quebrada La Tostada, vía hacia la hacienda San Antonio, 05°32′53.78″N, 74°51′42.3″W, 234 m, *D. Sanín 4471* (COL, FAUC); ibid., Vereda La Quiebra (de Roque), cañon del Río Moro, Camino Real a Planes del Mirador, 05°34′02.6″N, 74°54′06.2″W, 460 m, *A. Duque 2726* (HUA); Victoria, Vereda doña Juana alta, unos 3 Km de la variante a Samaná, 06°00′N, 74°45′W, *R. Sanchez 3901* (COL). **Córdoba:** Tierra Alta, Ciudadela Urrá S.A., cerro detrás de la bocatoma, 08°06′21.68″N, 76°03′01.18″W, 320 m, *R. Fonnegra 7999* (HUA). **Tolima:** Mariquita, bosque a 2 km al SO del pueblo, [ca. 05°11′24″N, 74°54′41″W] 550 m, *R. Bernal 806* (COL).

The hairs on the laminae of *Cyathea paisa* are often covered in black acicular fruiting bodies of an unidentified fungus.

The specimen *P.V. Trujillo-Q. 7706* (HUA) has extraordinarily large pinnules but matches *Cyathea paisa* otherwise all aspects, thus it is included in this species. The size of the pinnules is more reminiscent of Colombian *C. acutidens*.

9. *Cyathea pinnula* (Christ) Domin, Pteridophyta: 263. 1929. *Cyathea pinnula* (Christ) R. C. Moran, Novon 1: 90. 1991, *nom. illeg. Alsophila pinnula* Christ, Prim. Fl. Costaric. 3: 43. 1901. Type.—COSTA RICA. Limón: Río La Matina, 20 m, Sept 1896, *H. Pittier 10267* (holotype: P-00633155 [Herb. Christ]!; isotypes: BR-0000006978679 [image!], MICH [photo P], NY [fragm. ex P], P-00633154!, US-00066214/-01100760 [image!]). **Figs. 1J, 15.**

Trunks 0.5–2.5 m, erect, 5–8 cm diam., with persistent old petioles; adventitious buds absent. *Leaves* 1.1–2.0(–3.1) m long, erect, *i.e.*, held at an acute angle towards the trunk axis, distally arching; expanding subsequently. *Petioles* 30–54 cm long, inermous to sparsely aculeate with blunt spines to 4 mm long, green to yellowish in young leaves, dark brown to vinaceous in old ones, matte to weakly shiny, scurf absent or scarce, consisting of tan trichomidia, soon shed. *Petiole scales* 15–35 × 3–5 mm, lanceolate to long lanceolate, apices weakly undulate, concordantly bicolorous dark castaneous with golden brown to yellowish margins. *Rachises* sparsely aculeate with scattered prickles to 3 mm long, rarely inermous, brown to vinaceous, with multicellular hairs to 1.0 mm long, densely pubescent adaxially with hairs tan and antrorsely curved, less pubescent abaxially with hairs whitish, flaccid, spreading. *Laminae* 80–160(–230) × 30–90 cm, long ovate, bipinnate-pinnatifid, ca. 15 pinna pairs, alternate, apices gradually reduced to abruptly reduced to a non-conform apical section. Largest *pinnae* to 45 × 14 cm, pinnae sessile to stalked to 1 cm, 8–10(–14) pairs per leaf, alternate, patent to weakly ascending, distally broadly green-alate between the pinnules/segments, apices acute to attenuate; basal pinnae about 2/3 the length of longest pinnae, weakly reflexed. *Costae* and *costules* inermous, green or yellowish to brown, adaxially darker than abaxially, densely pubescent adaxially with hairs whitish to pale brown, 0.6–0.8 mm long; antrorsely curved, sparsely to densely hairy abaxially, with erect white multicellular hairs to 0.5 mm long; costae 1.5–2.0 mm wide; junctures of costae and rachises not or weakly swollen abaxially, each with a planar to weakly raised pneumathode, to 3 × 2 mm, often black in dried specimens. Largest *pinnules* 45–70 × 9–15 mm, pinnules sessile to subsessile with stalks to 1.0 mm, oblong, bases truncate to weakly cuneate, tips acute to obtuse. *Costules* similar in color and indument to costae. *Segments* to 5.0–9.0 × 2.5–3.0 mm, ascending, straight or weakly falcate distally, their margins dentate-crenate or serrate, adaxially with few antrorsely curved white hairs (0.5–1.0 mm long) on the midveins, moderately to densely hairy abaxially with erect, white, multicellular hairs to 0.5 mm long on and between the veins, also with orange-brown to brown squamules to 0.5 mm long, mainly flat, few subbullate or bullate; sterile veins simple, fertile veins simple, rarely forked. *Sori* 0.8–1.0 mm diam., medial; indusia absent or hemitelioid, tan to brown, very small, often very narrow and forked like a fish-tail, reaching 1/5 or less around the receptacles, obscured by sporangia and paraphyses; receptacles globose, 0.2–0.3 cm diam., paraphyses few to many, evenly distributed on receptacles, whitish to tan, thin, usually longer than the sporangia (0.5–0.7 mm). *Spores* not examined.

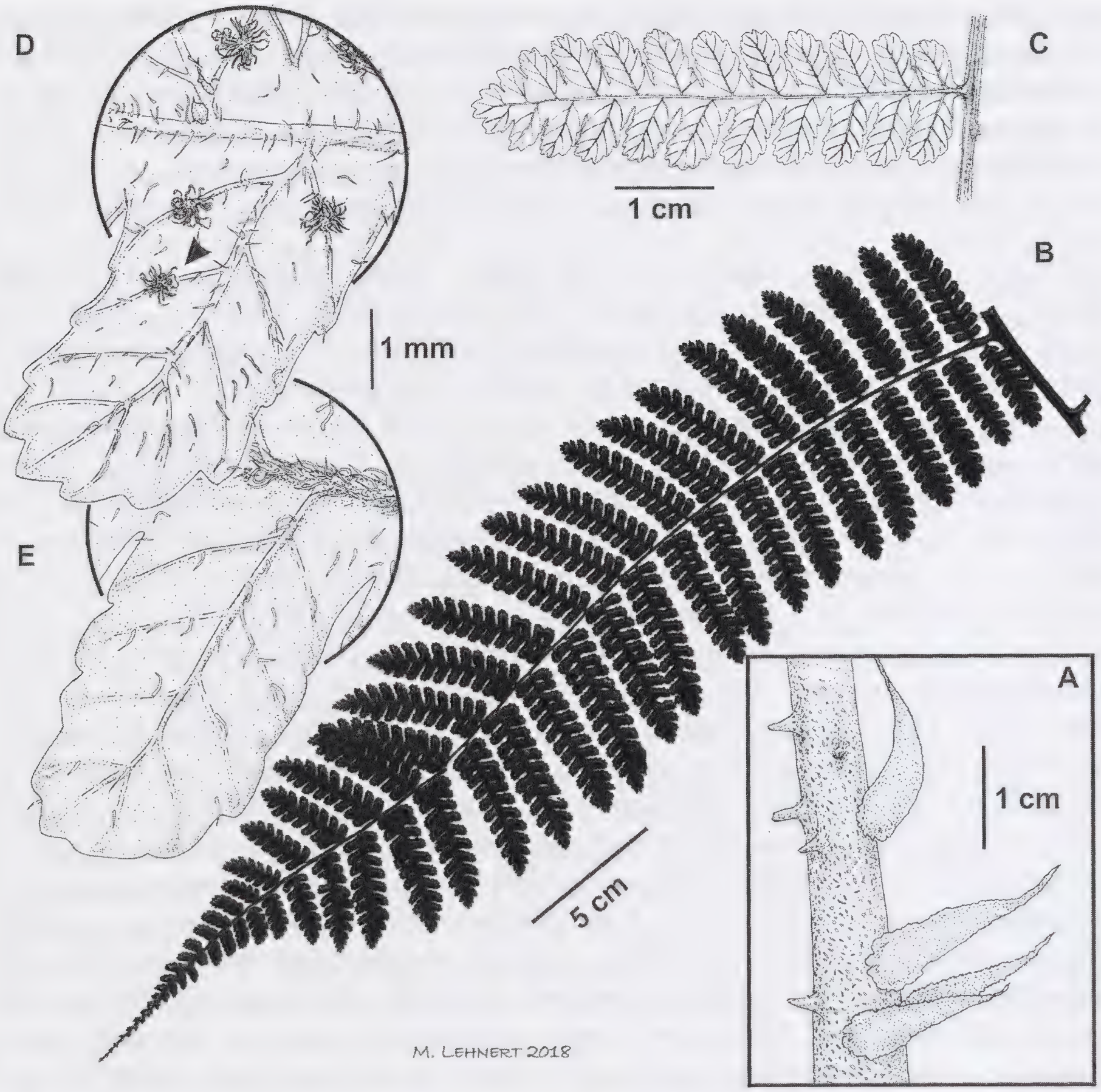

FIG. 15. *Cyathea pinnula*: A. Petiole with scales. B. Medial pinna, silhouette. C. Pinnule, adaxially. D. Segment, fertile, abaxially; arrow = small indusium. E. Segment, adaxially. (All drawn from *M. Lehnert 3503*, BONN)

DISTRIBUTION AND HABITAT.—Costa Rica to western Colombia (Antioquia) (Fig. 2B) in wet lower montane and lowland forests at 20–2000 m.

ETYMOLOGY.—The name probably alludes to the high number of small pinnules, as Christ (1901) mentioned "pinnules nombreuses", but no clear explanation is given.

ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. **Alajuela:** San Ramon, 1350–1500 m, 18 Feb 1983, *Carvajal A. 334* (UC); 17–20 km NNW of San Ramón by road on way to San Lorenzo, 4–7 km N of Balsas, 10°13′N, 84°32′W, 750 m, 24 Apr 1983, *R.L. Liesner. & E. Judzievicz 14701* (MO, UC); Univ. de San Ramón's Biological Field Station, ca. 20 km N of San Ramón, along Río San Lorencito, 10°15′N, 84°30′W, 800–900 m, 27 Feb 1988, *R.C. Moran 4133* (UC).

Guanacaste: Parque Nacional Rincon La Vieja, the SE slope of Volcán Santa María, above estación Hacienda Sant María, 10°47′N, 85°15′W, 900–1200 m, 27–28 Jan 1983, *G. Davidse et al. 23401* (MO, UC). **Heredia:** Parque Nacional Braulio Carillo, from La Montura to Los Chorritos, 1200 m, 28 Jan 1984, *L.D. Gómez, I. Chacón, & Herrera G. 20926* (UC); between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, 10°17.5′N, 84°04.5′W, 700–750 m, 05 Apr 1986, *M.H. Grayum & C. Jermy 6778* (MO, UC); Braulio Carillo National Park, 10°20′N, 84°10′W, 1000 m, 14 Nov 1986, *E. Hennipman, M.C. Roos, G.P. Verduyn & P. Veldhoen 6900* (UC). **Limon:** Cantón de Limon, Cordillera de Talamanca, N flank of Fila de Matama in headwaters of Río Boyei, 09°45′N, 83°19′W, 1200–1300 m, 15 Aug 1995, *M. Grayum 10792* (MO); Cantón de Limon, Cordillera de Talamanca, along divide between Río Xikiari and Río Boyei above Cabécar village of Almirante, 09°46′30"N, 83°20′00"W, 1100–1150 m, 13 Aug 1995, *M. Grayum 10908* (MO, UC); Cordillera de Talamanca, N flank of Fila de Matama in headwaters of Río Boyei, 09°45′N, 83°19′W, 1200–1300 m, 15 Aug 1995, *M. Grayum 10972* (MO, UC).

PANAMA. **Chiriquí:** Fortuna Dam area, N fork of the Quebrada de Arena, 08°46′N, 82°12′W, 1100 m, 06 Feb 1984, *H.W Churchill, G. de Nevers & H. Stockwell 4674* (MO, UC); vicinity of Fortuna Dam in valley of Río Chiriquí, along aqueduct trail for water supply for IRHE facilities, 08°45′N, 82°18′W, 1100-1200 m, 21 Jun 1987, *T.B. Croat 66590* (UC); area E of mining camp at dam site, Fortuna Dam site, 1500 m, 14 Sep 1977, *J.P. Folsom, R. Dressler & K. Dressler 5450* (UC, MO); Road Almirante - Chiriquí, 08°44.746′N, 82°12.649′W, 1180 m, 06 Jan 2016, *M. Lehnert 3503* (PMA, BONN). **Veraguas:** Cerro Mariposa, near Santa Fé, 08°30.404′N, 81°00.159′W, 1050 m, 08 Jan 2016, *M. Lehnert 3520* (BONN, PMA).

COLOMBIA. **Antioquia:** San Luis, vereda Manizales Finca Ramón Jaramillo, 1460–1760 m, *C. Orozco 542* (COL); Frontino, Parque Nacional de Las Orquídeas, Finca La Guaduala, quebrada Horacio, afluente del Río Venados. 5.3167000 N, -76.2625889 W, 1160 m, 1 Dec 1986, *R. Callejas 2939* (HUA); Guatapé, vereda Santa Rita, Fca. Montepinar, 6.5000000N, -75.5333333 W, 1850 m, 24 Apr 1990, *N. Contreras 285* (HUA); Frontino, Región de Murri, 12 Km de Nutibara, bosque al borde del camino, 6.2500000 N, -75.1666667 W, 2150 m, 11 Dec 1988, *G. McPherson 13460* (HUA); Valdivia, vereda San Fermín, bosque Montenegro, 2056 m, Aug 2009, *L. Urrea 342* (HUA), ibid., *L. Urrea, 343* (HUA); Yarumal Vía hacia el Cedro, cerca a la entrada, 1900 m, 20 Dec 2001, *F. Giraldo 2582* (HUA, JAUM). **Chocó:** Región del Corcovado, sobre el Río San Juan, 200–275 m, 24 May 1939, *E.P. Killip 35279* (COL); Banks of Quebrada de Togoroma, Chocó, [ca. 04°21′09.5"N, 77°21′54.3"W] 13 Jun 1944, *E.P. Killip 39084* (COL, US, VALLE); Tutunendo, W of Tutunendo, Quibdo-Medellin road, 5.7500000 N, -76.5333333 W, 100 m, *A. Gentry 36866* (JAUM, MO).

The laminae of *Cyathea pinnula* are sometimes covered abaxially with black acicular fruiting bodies of an unidentified fungus.

Moran (1991) resurrected the name *Cyathea pinnula* from the *nomina incertae sedis* of the exindusiate *Cyathea* species, revised as *Trichipteris*

(Barrington, 1978). Closer examination of the cited material (Moran, 1991) revealed the presence of a vestigial indusium in *C. pinnula*, recognizable as a small, brown, scale-like structure. This showed further relatedness to *C. multiflora sensu lato*, besides the matching pinnule proportions and marginal indentation.

As a specimen, *Cyathea pinnula* is superficially similar to a number of sympatric species, which all have easily recognizable indusia (*i.e.*, *C. austroamericana, C. hildegardis, C. pinnuloides*). Besides having almost no indusia, *Cyathea pinnula* is also characterized by regularly having few scattered prickles on the rachis and by comparatively small pinnules with rather blunt tips. See *C. pinnuloides* for more discussion.

10. ***Cyathea pinnuloides*** Lehnert, F.Giraldo & W.D.Rodr., **sp. nov.** Type:—COLOMBIA. Antioquia: Amalfi, carretera que conduce a la Vereda Guayabito, 06°53′28.23″N, 75°04′24.47″W, 1750–1850 m, 17 Apr 2000, *F. Giraldo 2044* (holotype: HUA!; isotype: JAUM!). **Figs. 5G–K, 16.**

Diagnosis.—Cyathea pinnuloides can be distinguished from other species of the *C. multiflora* alliance by the prevailing strongly bullate, orange squamules abaxially on the costules while other superficially similar species like *C. columbiana* or *C. multiflora* have either only flat squamules or weakly bullate squamules.

Trunks 0.5–1.7 m, 3–4 cm diam., with persistent old petioles; adventitious buds absent. *Leaves* (1.1–)1.5–2.8 m long, arching from ascending petioles; expanding subsequently; sometimes covered abaxially with black acicular fruiting bodies of a fungus. *Petioles* (10–)38–70 cm long, inermous to sparsely tuberculate, green to yellowish in young leaves, dark brown to brown in old ones, always opaque, scurf absent or scarce, consisting of scattered brown squamules, soon shed. *Petiole scales* 12–15 × 9–10 mm, broadly lanceolate, apices acute to attenuate, weakly undulate to weakly twisted, shiny, varying from ± concordantly bicolorous dark castaneous with golden brown to yellowish margins to almost concolorous orange–brown. *Leaf axes* [rachises, costae & costules] inermous, green to brown, with multicellular hairs 0.5–0.7 mm long, densely pubescent adaxially with hairs tan and antrorsely curved, less pubescent abaxially with hairs tan to whitish and spreading, becoming paler and longer (to 1 mm) abaxially on costules. *Laminae* 110 × 62cm, long ovate to elliptic, bipinnate-pinnatifid, apices gradually reduced, rarely a conform pinna-like section. Largest *pinnae* 30–45 × 7 cm, pinnae sessile to stalked to 1 cm, 18–20 pairs per leaf, alternate, patent to weakly ascending, distally broadly green-alate between the pinnules/segments, apices acute to attenuate; basal pinnae 2/3–3/4 the length of longest pinnae, weakly to strongly reflexed. *Costae* 1.5–2.0 mm wide; junctures of costae and rachises not or weakly swollen abaxially, each with a planar to weakly raised pneumathode, to 2 × 1 mm, often black in dried specimens, also covered with strongly bullate orange squamules to 1 mm long, with short subulate tips. Largest *pinnules* 29–38 × 7.0–7.5 mm, pinnules sessile to mostly subsessile

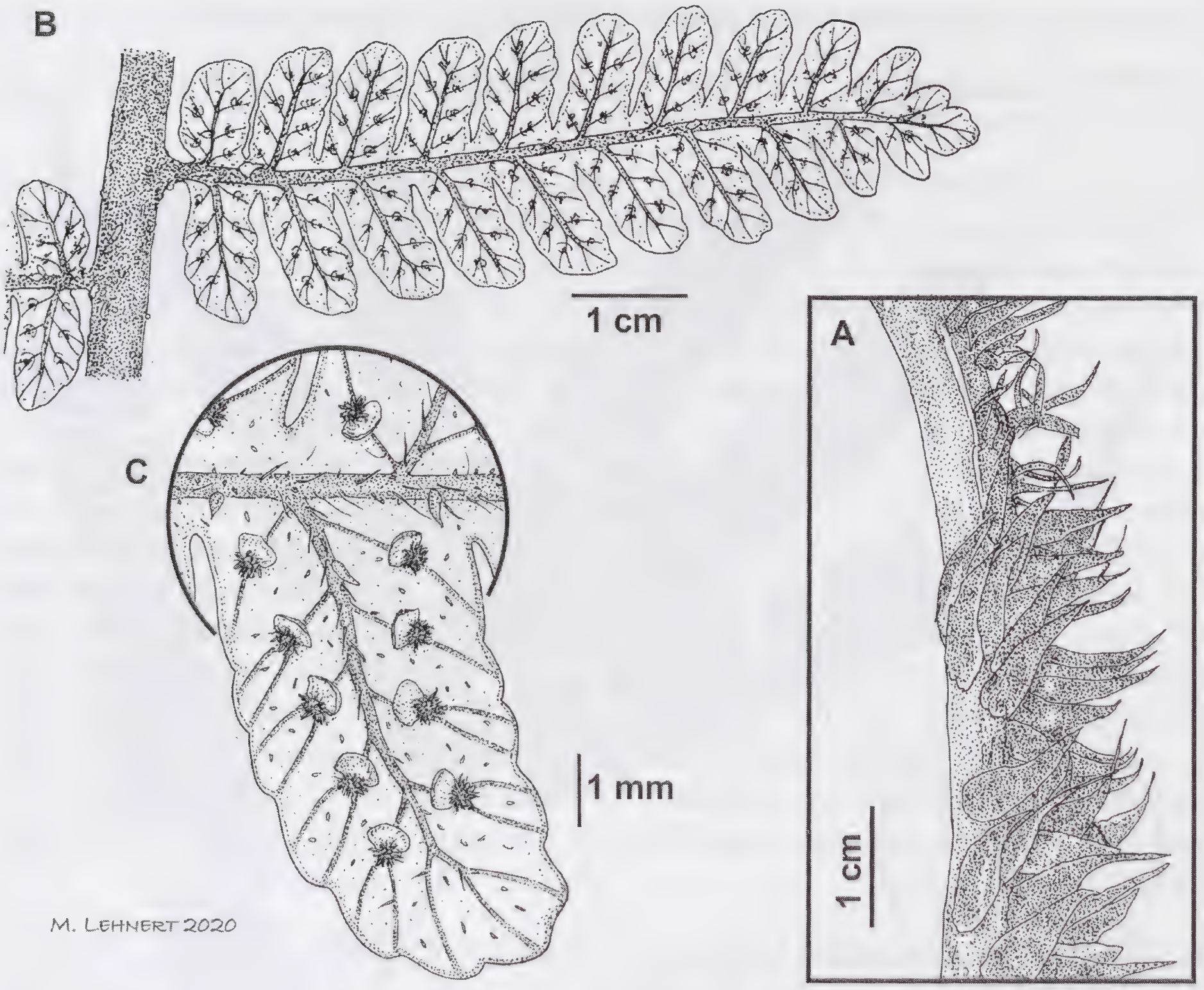

FIG. 16. *Cyathea pinnuloides*: A. Petiole with scales. B. Pinnule, fertile, abaxially. C. Segment, fertile, abaxially. (All drawn from *F. Giraldo 2044*, holotype, HUA)

with stalks to 1.0 mm, oblong, bases truncate to weakly cuneate, tips obtuse to short-acute. *Costules* abaxially with few to many orange-brown to orange squamules 0.5–1.0 mm long, mainly strongly bullate with subulate tips, few sub-bullate or flat. *Segments* to 4.0–5.5 × 2.0–2.5 mm, ascending, straight or weakly falcate distally, their margins dentate-crenate or serrate; sinuses acute, narrow, to 0.5 mm wide; adaxially with few antrorsely curved tan hairs (0.5–1.0 mm long) on the midveins, moderately to densely hairy abaxially with erect, white, multicellular hairs to 1.0 mm long on the veins, few between them below sinuses, veins also with appressed white trichomidia, with orange-brown to orange squamules 0.5(–1.0) mm long, mainly strongly bullate with subulate tips, few sub-bullate or flat; sterile veins simple, fertile veins simple, rarely forked. *Sori* 0.8 mm diam., medial; indusia hemitelioid, tan to brown, reaching 1/4 or less around the receptacles, hidden in entire sori; receptacles globose, 0.2(–0.3) mm diam., paraphyses few, evenly distributed on receptacles, whitish to tan, bases turgid, apices catenate, longer than sporangia (0.4–0.5 mm). *Spores* not examined.

Etymology.—The name refers to the similarity to *Cyathea pinnula*.

Distribution and habitat.—Northwestern Colombia (Antioquia) (Fig. 2C) in wet lower montane forests at 1700–2000 m.

Additional specimens examined (Paratypes).—COLOMBIA. **Antioquia:** Valdivia, Vereda San Fermín, Finca San Fermín, 07°05′51.37″N, 75°25′54.04″W, 1800–2000 m, 29 Mar 1988, *A. Arbeláez 295* (HUA); Yarumal, Vda. Alto de Ventanas, vía que conduce al Mpio de Briceño, 07°05′05″N, 75°29′30″W, 1770–1965 m, 14 Sep 2015, *F. Giraldo 3145* (HUA); Frontino, Alto de Carauta, Corregimiento de Nutibara, Vereda el Guayabo, 06°41′20.5″N, 76°12′59″W, 11 Feb 2016, 1720 m, *F. Giraldo 3742* (HUA).

Specimens of *Cyathea pinnuloides* and *C. pinnula* are relatively well represented in herbaria but had been kept under a broadly defined *C. multiflora* (Tryon, 1976). *Cyathea pinnuloides* on average has smaller pinnules but larger, more evident indusia than *C. pinnula* (reduced to a fish-tail like structure barely recognizable among paraphyses). The presence of pinna-like apices in *C. pinnuloides* does not seem to be constant. In *C. multiflora* and *C. retanae* (Fig. 11 F. K), we also find varying leaf apex morphologies in one population and even in single plants. This variability seems to be a common feature of the species here addressed as members of the *C. multiflora* alliance, just like the black acicular fungal fruiting bodies regularly encountered on the hairs.

11. ***Cyathea prosopioides*** Lehnert, F.Giraldo & A.Tejedor, **sp. nov.** Type.—COLOMBIA. Risaralda: Municipio Mistrato, corregimiento Puerto de Oro, vía Pisones-Geguadas (= Río Mistrato), 800–1400 m, 20 Sep 1991, *J.L. Fernández Alonso, C.I. Orozco, P. Franco, J. Betancur et al. 9143* (holotype: COL-000285372!). **Fig. 17.**

Diagnosis.—Cyathea prosopioides is most similar to *C. bipinnata* in having ascending linear pinnae and a matching pinna-like apical section but differs in the indentation of the laminar margin, which is distinctly inciso-serrate in *C. prosopioides*, especially in the caudate pinna tips, and subentire to weakly crenate in *C. bipinnata*. From *C. uregoana*, *C. prosopioides* differs in having pale petiole scales (entirely white or with pale brown margins in *C. prosopioides* vs. dark castaneous brown in *C. uregoana*).

Trunks to 0.7 m, decumbent, otherwise unknown. *Leaf* dimensions unknown [estimated to be to 2 m long, held erect]. *Petioles* at least 33 cm long, inermous, brown in dried material, matte, on each side with one line of narrow pneumathodes to ca. 30 × 2–3 mm (shrunken and inconspicuous in dried material); scurf a thin, amorphous layer consisting of pale to orange-brown branched hairs and lacerate squamules less than 1 mm long, easily shed. *Petiole scales* to 20 × 3–5 mm, lanceolate to ovate-lanceolate, concolorous white to discordantly bicolorous, golden brown with wide white margins, these soon worn off. *Laminae* 25 cm wide, long ovate to elliptic, bipinnate-pinnatifid, apices abruptly reduced, pinna-like, with ca. 18–

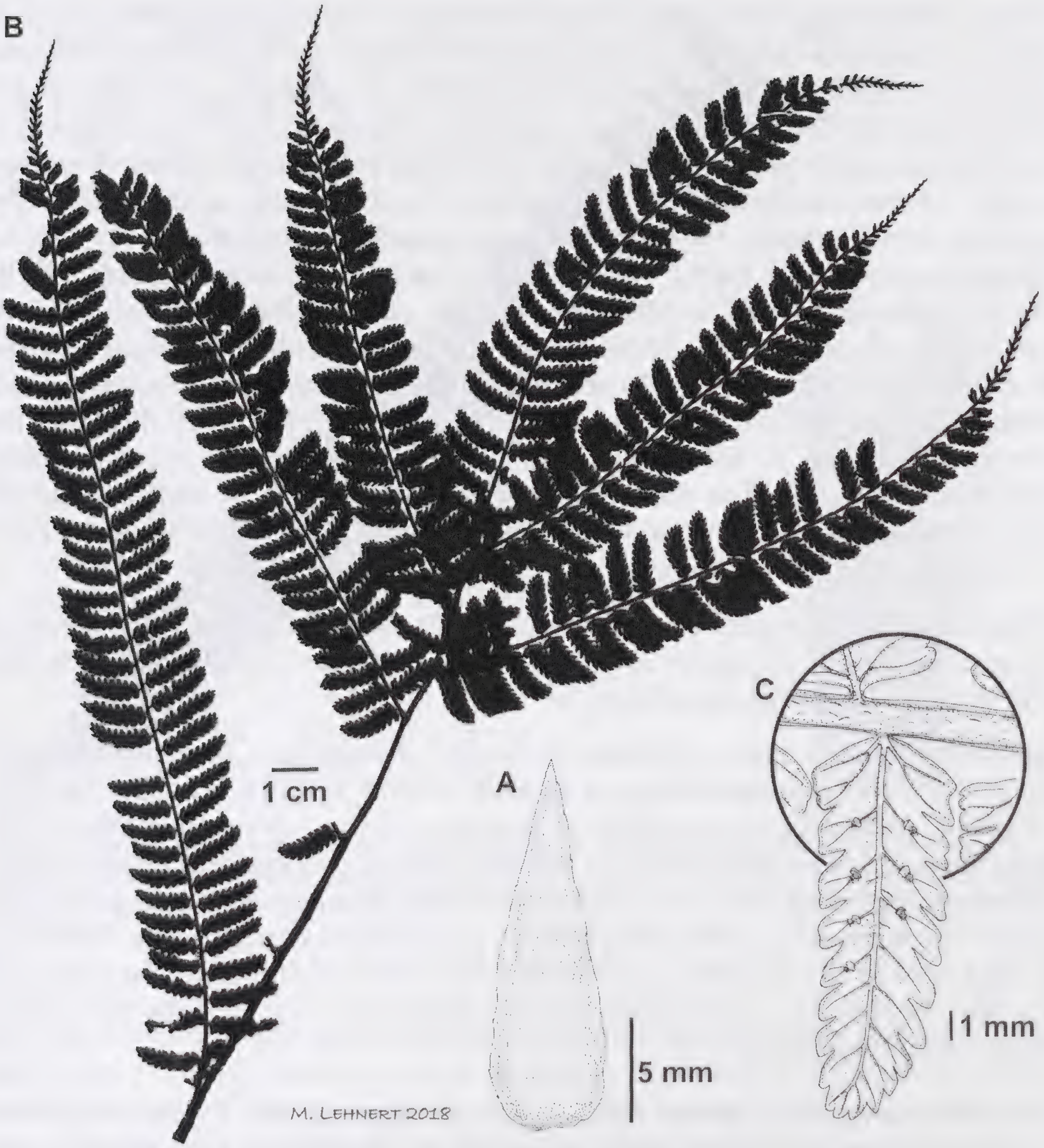

FIG. 17. *Cyathea prosopioides*: A. Petiole scales. B. Upper half of leaf, some pinnae missing, silhouette. C. Segment, fertile, abaxially. (All drawn from *J.L. Fernández Alonso et al. 9143*, holotype COL).

24 (–34) pinna pairs, basal pinnae not seen. *Rachises* inermous, brown, densely short pubescent on both sides, hairs to 1 mm long, retrorsely curved, adaxially reddish brown to brown, abaxially yellowish white. Largest *pinnae* ca. 25 × 3 cm, pinnae linear, tapering only in distal 1/5, apices attenuate to caudate, green-alate throughout between the pinnules/segments, pinnae alternate, weakly ascending (ca. 70°–60° towards the rachis). *Costae* inermous, costae pubescent on both sides, the hairs 0.6–0.8 mm long, adaxially reddish brown, antrorsely curved, abaxially whitish, retrorsely

curved. *Pinnules* to 15 × 3 mm, sessile, articulate, oblong, truncate to rounded basally, rounded to obtuse apically; pinnules lobed only to ca. 1/2 towards the costules. *Costules* inermous, adaxially glabrous or nearly so except for single white hairs distally, abaxially with appressed to erect, pale brown to white multicellular hairs to 0.5 mm long; flat or bullate squamules absent. *Segments* to 3.0 × 1.5 mm, ascending, straight, without clear midvein, each supported by a simple or once (rarely twice) forked vein, segment margins coarsely serrate, sinuses acute, narrow (to 0.8 mm wide), no hairs on or between veins; sterile veins simple or forked, fertile veins forked, contrasting dark with laminar tissue. *Sori* ca. 0.6–0.8 mm diam., medial in respect with the costules, in fork of lateral veins, each with ca. 20 sporangia; indusia hemitelioid, brown, small, reaching 1/4 to 1/5 around the receptacles, not arching over the sori, the margins subentire or weakly dentate; receptacles globose, 0.2 cm diam., paraphyses few, tufted at the tips of the receptacles, tan to white, relatively thick, complanate, of the same length as the sporangia or slightly shorter (0.2–0.3 mm). *Spores* not examined.

Etymology.—The name alludes to the similarity of the pinna with the leaves of the mesquite bush (*Prosopis sp.*; Fabaceae), which are both linear in outline with evenly sized primary segments.

Distribution and habitat.—Western Colombia (Risaralda; Chocó region) (Fig. 2C) in wet lower montane forests at ca. 800–1400 m; only known from the type.

Cyathea prosopioides resembles *C. uregoana* in the linear pinna shape with long tapering apices and distinctly crenate margins but matches better with *C. bipinnata* regarding the leaf architecture with abruptly reduced, pinna-like apices. We have only a rather fragmentary specimen at hand, but the difference in thickness of the available petiole and the rachis of the distal laminar part can only be bridged if the whole leaf is about 2 m long at least, provided a regular gradual tapering.

12. ***Cyathea uregoana*** Lehnert, F.Giraldo & A.Tejedor, **sp.nov.** Type: COLOMBIA. Chocó: 0.5 km N of San José del Palmar on the slope behind the cemetery, [ca. 04°53′52″N, 76°14′07″W] 1110 m, 26 Mar 1971, *D.B.Lellinger & E.R. de la Sota 732* (holotype: COL-000006214!, isotypes CR n.v., HUA-3967!, US-01452193/-01452197 [2 sheets, image seen], LP n.v.). **Figs. 5L–N, 18.**

Trichipteris uregoana Lellinger, *nom. nud.*

Diagnosis.—Cyathea uregoana has relatively narrow, notably rectangular laminae with 18–34 pinna pairs and a clearly acuminate apex, thus differing from *Cyathea columbiana*, the most similar sympatric species, which has ovate laminae with up to 10 pinna and more gradually reduced apices.

Trunks 0.8–2.0 m, to 5.0 cm diam., with persistent old petioles, but these rotting off, hence trunk generally appearing rough and irregularly thick, sometimes with cleared areas showing leaf scars; trunk apices hidden in fascicle of petioles; adventitious buds absent. *Leaves* 1.3–2.4 m long, arching, distally drooping, expanding subsequently; often covered abaxially with black

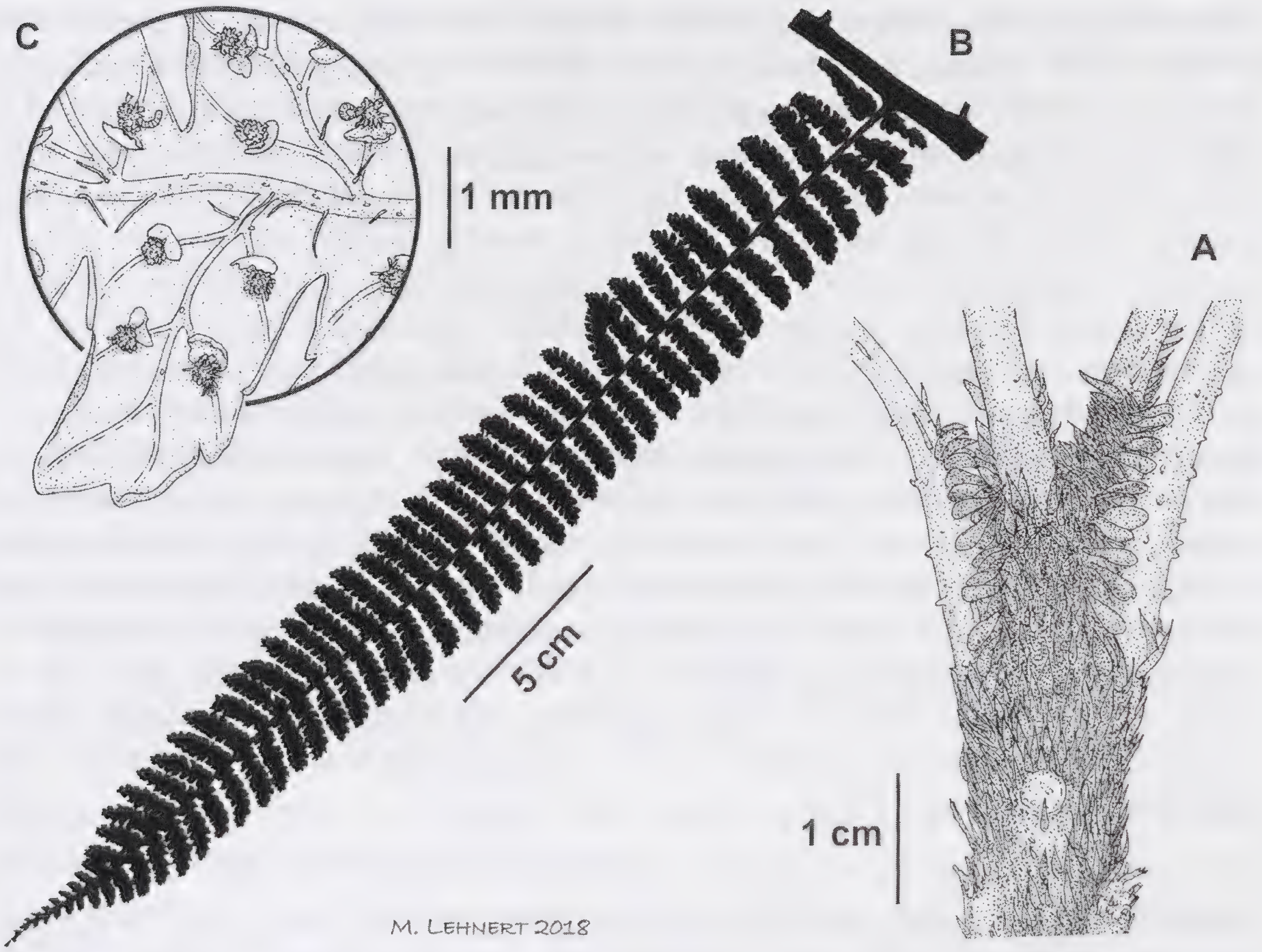

FIG. 18. *Cyathea uregoana*: A. Trunk apex and petioles with scales. B. Medial pinna, silhouette. C. Segment, fertile, abaxially. (A. drawn from photo of *F. Giraldo 3022*, HUA; B–C. drawn from *D.B. Lellinger & E.R. de la Sota 892*, holotype COL)

acicular fungal fruiting bodies, especially abaxially on thinner leaf axes, veins and hairs. *Petioles* 15–55 cm long, inermous to sparsely aculeate (to 2 mm long), green to yellowish in young leaves, dark brown to brown in old ones, always matte, with one line of narrow white pneumathodes, each to 15 × 2 mm (shrunken and often inconspicuous in dried material); scurf a thin, amorphous layer consisting of pale to orange-brown branched hairs and lacerate squamules less than 1 mm long, soon shed. *Petiole scales* to 20 × 3–5 mm, lanceolate to ovate-lanceolate, the apices weakly undulate, discordantly bicolorous, dark castaneous with paler to golden brown, narrow margins, often worn off. *Rachises* inermous, green to brown, densely short pubescent adaxially, with hairs to 1 mm long, erect, sparsely pubescent to glabrescent abaxially, sometimes with remnants of orange-brown scurf. *Laminae* 80–195 × 40–90 cm, long ovate to elliptic, bipinnate-pinnatifid, basal pinnae not or just weakly reflexed, apices gradually reduced, sometimes acuminate. Largest *pinnae* 35–45 × 3.5 cm, pinnae sessile, alternate, ca. 18–24 (–34) pairs per leaf, linear, tapering only in distal 1/5, apices attenuate to caudate, green-alate throughout between the pinnules/segments, pinnae alternate, weakly

ascending (ca. 70° toward the rachis). *Costae* inermous, adaxially pubescent, the hairs pale brown, antrorsely curved, 0.6–0.8 mm long, abaxially glabrous. *Pinnules* to 16 × 5 mm, sessile, articulate, oblong, truncate basally, rounded to obtuse apically. *Costules* inermous, adaxially pubescent like costae, abaxially with appressed to erect, pale brown to white multicellular hairs to 0.5 mm long and few orange-brown to brown flattish or weakly bullate squamules 0.5–1.5 mm long. *Segments* to 3.0 × 1.5 mm, ascending, straight, their margins coarsely serrate, sinuses acute, narrow (to 1 mm wide), glabrous adaxially except for one to two antrorsely curved hairs (0.5–1.0 mm long) on veins, abaxially midveins with few short hairs like those on costules; glabrous between veins except for occasional trichomidia (0.2 mm long); sterile and fertile veins simple, contrasting dark with laminar tissue. *Sori* ca. 0.8 mm diam., proximal (rarely subproximal), in fork between midveins and simple lateral veins; indusia hemitelioid, brown, large, reaching 1/3 to 1/2 around the receptacles, arching over the sori, more or less hemispherical, the margins subentire or weakly dentate; receptacles globose, 0.2–0.3 cm diam., paraphyses few to many, tufted at the tips of the receptacles, tan to brown, relatively thick, complanate, of the same length as the sporangia (0.3–0.4 mm). *Spores* not examined.

Etymology.—"Urego" is a Spanish surname. The epithet for this new species was designated by D. B. Lellinger, which he never published, having come to the conclusion that the species matches the already published *Cyathea columbiana* Domin (= *Cyathea multiflora sensu* Tryon, 1976). Although Lellinger was not able to explain the reference anymore, we have grown accustomed to the name and feel inclined to bestow the honor to the unknown person whom Lellinger deemed worthy enough half a century ago.

Distribution and habitat.—Western Colombia (Chocó-region) (Fig. 2C) in wet lower montane forests at 230–1110 m.

Additional specimens examined (paratypes).—COLOMBIA. **Chocó:** 0.3 km E of the Ciudad Bolivar-Quibdo road across the suspension bridge at ca. Km 141, [ca. 05°44′45"N 76°17′18"W] 750 m, 03 Apr 1971, *D.B. Lellinger & E.R. de la Sota 892* (HUA, US-01452192/-01452198). **Valle del Cauca:** Old road Dagua-San Buenaventura, 03°38.212′N, 76°56.560′W, 230 m, 09 Feb 2015, *M. Lehnert 3102 with F. Giraldo, W.D. Rodríguez, M. Kessler* (BONN, HUA, Z).

In the northern Andes, *Cyathea uregoana* and *C. columbiana* are easily distinguished from the Mesoamerican *C. multiflora sensu stricto* by their large indusia (reaching 1/3–1/2 around the receptacle, arching over sporangia vs. 1/4 or less, hidden by sporangia in *C. multiflora*), narrow linear pinnae (vs. more lanceolate), and small blunt tipped pinnules (less than 30 × 6 mm vs. more than that). These two taxa had been recognized by Lellinger as one, *Cyathea columbiana* Domin, after he had intended to describe it as *Trichipteris uregoana*. Our field studies, however, have convinced us that these are two separable sympatric species, with distinct appearances in the field (Fig. 5A–C, L–N). *Cyathea columbiana* holds its relatively stiff leaves

more erect to patent and has less than 15 pinna pairs per leaf; *Cyathea uregoana* has arching leaves with drooping apices and usually more than 15 (up to 34) pinna pairs. *Cyathea uregoana* further has very small pinnules (≤2 cm), relatively broadly ovate-lanceolate petiole scales, and wholly alate costae.

New Record

13. *Cyathea retanae* A.Rojas, Mét. Ecol. Sist. 3(1): 43. 2008, *nom. nov.* for *Cyathea affinis* A.Rojas, Mét. Ecol. Sist. 2(3): 2. 2007, not *Cyathea affinis* (G.Forst.) Sw., J. Bot. (Schrader) 1800 [2]: 94. 1801, not *C. affinis* M.Martens & Galeotti, Nouv. Mém. Acad. Roy. Sci. Bruxelles 15(5): 80. 1842, not *Cyathea affinis* Brack., U.S. Expl. Exped., Filic. 16: 283. 1854. Type.—PANAMA. Darién: Parque Nacional de Darién, Panama/Colombian border, near gold mine at head waters of N branch of Río Pacuro, slopes of Cerro Tacarcuna, ca. 6 km N of Cerro Mali, 08°09.5′N, 77°15′W, 1300–1500 m, 27 Oct 1987, *G. Nevers et al. 8529* (holotype: MO-2114217!). **Fig. 11K**

Distribution and habitat.—Panamá and northwestern Colombia (Chocó) (Fig. 2B) in wet ridge forests at 1100–1500 m.

Additional specimens examined.—COLOMBIA. **Chocó:** Mun. Ungüia, Vereda Arqua, cabeceras del Río Arqua, sector Cielo Azul, Cerro Tacarcuna, frontera con Panamá, 08°02′38.0″N, 77°13′28.9″W, 1100 m, 2 Apr 2017, *F. Giraldo 3792* (HUA); *ibid.*, 08°02′30.1″N, 77°13′34.0″W, 1279 m, 4 Apr 2017, *F. Giraldo 3833* (HUA); *ibid.*, 1279 m, 4 Apr 2017, *F. Giraldo 3834* (HUA).

Cyathea retanae was specifically sought and found on the Colombian side of Cerro Tacarcuna, a mountain shared with Panamá and sole known locality of the species (Fig. 2B).

The species has a peculiar indusium that does not reach all around the receptacle but covers the intact sorus. The hemitelioid ("incomplete") condition is only revealed once the sporangia break the indusia upon opening. Such hood-like indusia are not rare among Australasian *Alsophila* but are otherwise found in neotropical *Cyathea* only in the Galapagos Island endemic *C. weatherbyana*; approaching this shape are the large hemitelioid indusia of *C. rojasiana* and *C. impar* (Lehnert and Weigand, 2017), both from Panama, and maybe also in western Colombia.

Cyathea retanae can be found in the undergrowth of very wet ridge forests; with its dark green glossy lamina and dark shiny leaf axes, it has the appearance of *Alsophila erinacea* (H.Karst.) D.S.Conant or *A. cuspidata* (Kunze) D.S.Conant, two neotropical tree ferns very common in closed forest. *Cyathea retanae* is easily separated by having wider, more ovate scales that lack marginal setae (vs. narrowly lanceolate to linear, with at least one black apical seta in *A. erinacea*, also additional marginal ones in *A. cuspidata*), and the lack of black brittle prickles on the petioles.

KEY TO THE SPECIES OF *CYATHEA* WITH HEMITELIOID INDUSIA AND BIPINNATE-PINNATIFID LEAVES IN COLOMBIA AND NEIGHBORING COUNTRIES

Species treated here in detail are in bold face.

1. Largest pinnules elliptic to oblanceolate with obtuse to rounded tips; veins regularly partially anastomosing . . . . . *C. bradei*
1. Largest pinnules mostly lanceolate or if oblanceolate then with acute to attenuate tips; veins not anastomosing 2
    2. Petiole scales narrowly lanceolate to lanceolate, 10.0–25.0 × 1.0–3.0(–3.5) mm, differentiated margin only developed near base, in distal parts reduced to one line of teeth . . . . . 3.
        3. Laminae obovate, often basally tapering with basal pinnae of the same size and dissection as the pinnules of largest pinnae, petioles then virtually absent; paraphyses of the same length as or shorter than the sporangia . . . . . *C. cyatheoides*
        3. Laminae ovate-elliptic, basally not gradually tapering, petioles well developed paraphyses longer than the sporangia, forming a dense mass in over-mature sori 4
            4. Petiole scales ± concolorous reddish brown; petiole and axes without whitish scurf; laminar squamules ample and dark brown, indusium virtually absent, reduced to a filiform structure . . . . . *C. macrosora*
            4. Petiole scales discordantly bicolorous stramineous with darker center; petiole and axes with easily abraded whitish scurf; laminar squamules sparse and pale brown; indusium well developed but hidden under paraphyses . . . . . *C. traillii*
    2. Petiole scales ovate-lanceolate to lanceolate, to 35.0 × 3.5–4.0 mm, differentiated margins relative wide, sometimes abraded 5
        5. Petiole bases with multicellular hairs all around, sometimes hidden between petiole scales 6
            6. Larger petiole scales almost concolorous blackish brown with narrow, slightly paler margins; most central pinnae notably stalked, gap between rachis and first pinnule ± width of that pinnule . . . . . *C. rojasiana*
            6. Larger petiole scales pale, completely or at least largely whitish, centers and bases may be darker but always discordantly bicolorous; most central pinnae subsessile, if gap between rachis and first pinnule then much less than width of that pinnule 7
                7. Petiole scales near petiole base strongly bicolorous, dark brown center with whitish margins, scales reaching up to lower rachis, long persistent; laminae obovate-elliptic, notably tapering basally; veins hairy only abaxially except for few scattered hairs on midveins adaxially; hairs abaxially on costules to 1 mm long, not reaching basal sori if flattened . . . . . ***C. acutidens***
                7. Petiole scales mostly white, near petiole base with dark spot (trunk scales sometimes strongly bicolorous), scales restricted to petiole base, not reaching lower rachis; laminae ovate-elliptic, basally not tapering; veins hairy on both sides, hairs abaxially on costules to 2 mm long, usually reaching basal sori if flattened . . . . . ***C. leucolepismata***
        5. Petiole bases without multicellular hairs, hairs absent or restricted to adaxial side of upper portions 8
            8. Sori closer to segment margins than to midveins (supramedial to submarginal) . . . 9
                9. Largest pinnae relatively long stalked; costules with whitish to orange–brown scaly indument, including small bullate squamules and some larger ovate scales, if scaly indument darker brown then abaxially with many short erect multicellular hairs on and between veins 10
                    10. Segment tips subentire to crenulate; scaly laminar indument whitish to pale brown; hairs abaxially absent or only sparse on veins, none abaxially on axes . . . . . *C andina*
                    10. Segment tips weakly dentate; scaly laminar indument mostly orange-brown; hairs abaxially abundant on and between veins, also extending on axes . . . . . ***C. retanae***

9. Largest pinnae relatively short stalked to sessile; costules with dark brown scaly indument, only strongly bullate squamules; abaxially without erect hairs (unicellular trichomidia may be present on and between veins) 11
11. Fertile plants without trunk, indusia small, hidden in intact sori, reaching 1/4 around the receptacle . . . . . ***C. mariposana***
11. Fertile plants with erect to decumbent trunk, indusia relatively large, visible in intact sori, reaching to 1/2 around the receptacle . . . *C. squamulosa*

8. Sori close to midveins to ± equidistant between segment midveins and margins (± medial if measured to the tips of the marginal lobes) 12
12. Petiole scales pale, orange-brown to completely or at least largely whitish, centers and bases may be darker but always discordantly bicolorous, *i.e.*, color of differentiated margin extending into scale body, leaving scales bicolorous even if margins are abraded 13
13. Petiole scales orange-brown to yellowish; segment margins serrate to double-serrate, segment tips acute, ending in triangular lobes; short erect hairs present on and between veins abaxially . . . . . ***C. paisa***
13. Petiole scales in most parts whitish; segment margins subentire to crenulate, segment tips blunt, not ending in triangular lobes 14
14. Pinnules small, oblong, shallowly lobed; laminar apex pinna-like . . . . . ***C. prosopioides***
14. Pinnules relatively large, the largest ones triangular-lanceolate, pinnatifid to pinnatisect; laminar apex gradually reduced 15
15. Scales appressed to trunk and petiole bases, most scales with well-developed dark brown to blackish center but obscured by paler margins due to imbricated layering . . . . . *C. holdridgeana*
15. Scales spreading from trunk and petiole bases, most scales concolorous stramineous to white, some with dark brown spot near base . . . . . *C. vilhelmii*

12. Petiole scales dark, completely dark reddish brown to castaneous or (rarely) blackish, differentiated margins varying from only slightly paler (mainly more translucent because of thinner texture) over yellowish to white, in latter case scales concordantly bicolorous, *i.e.*, marginal color restricted to differentiated margin and vanishing if margins are abraded 16
16. Petioles with reddish brown to orange-brown scurf 17
17. Squamules on costules flat to weakly bullate, scarce; rachises often weakly aculeate; indusia small, appressed to lamina but visible and persisting in over-mature sori . . . . . ***C. multiflora***
17. Squamules on costules strongly bullate, numerous; rachises inermous; indusia reduced, completely missing or a small lobe only visible after removal of receptacle (varies in one plant) . . . . . ***C. pinnula***

16. Petioles either without scurf or with whitish appressed lacerate squamules and branched hairs 18
18. Pinnules subsessile with weakly cuneate bases, with notable gap towards costa; squamules on costules strongly bullate, numerous; indusia relatively small, reaching 1/4 or less around the receptacles, appressed to lamina to weakly arching, shiny brown 19
19. Plants with decumbent to prostrate trunks; squamules on costules mainly flat, few subbullate; indusia often split in two, like a fishtail . . . . . ***C. hildegardis***
19. Plants with erect trunks; squamules on costules strongly bullate, numerous; indusia with entire, rounded margin . . . ***C. pinnuloides***

18. Pinnules sessile (to subsessile) with truncate to weakly cordate bases, not appearing remote from costa; squamules on costules flat to weakly bullate, scarce to absent; indusia relatively large, reaching 1/3–1/2 around the receptacles, arching, pale brown to gray 20

20. Pinnules relatively small, most blunt-tipped; sori proximal to submedial; indusia large, reaching 1/3–1/2 around the receptacles, arching over sori 21
    21. Sori when entire appearing subproximal, receptacle sitting on back of unbranched lateral vein, remote from midvein; 12–16 pinna pairs; pinnules to 45(–50) × 8(–12) mm . . . . . ***C. columbiana***
    21. Sori when entire appearing proximal, receptacles sitting in axil of midvein and unbranched lateral veins; 16–24 (–36) pinna pairs; pinnules to 16 × 5 mm . . . ***C. uregoana***
20. Pinnules relatively large, most with tapering tips; sori supramedial to submarginal; indusia small, reaching 1/4 to 1/5 around the receptacles, hidden by intact sori 22
    22. Relatively large plants, with trunks to 4(–10) m tall, (6–)10–15 cm diam., leaves with 12–16 pinna pairs; lamina abaxially glabrous or with few scattered hairs . . . . . ***C. lindigii***
    22. Small plants with trunks to 2(–3) m tall, 4–7 cm diam., leaves with 7–10 pinna pairs; lamina abaxially with many short hairs . . . . . ***C. paisa***

Acknowledgments

We thank our colleagues Michael Kessler, Gloria Calatayud, Marylaure de la Harpe, Adriana Hernandez, Jürgen Homeier, Oriane Loiseau, Julian Mostacero, Ingrid Olivares, and Anna Weigand for their company and help during fieldwork in Ecuador. Special thanks go to David B. Lellinger for sharing his memories, and Eric Schuettpelz who kindly mediated the communication with him. Asunción Cano, Ellúz Huaman and Blanca León kindly organized the collection permit for Peru. Collection permits were kindly issued by the Ministerio del Ambiente Ecuador (N° 036-2014-FLO-DP/MAE) and INRENA Peru (Resolución Directoral N° 0449-2010-DGFFS-DGEFFS). Esteban Domínguez Vargas kindly shared photos of *C. hildegardis* and *C. pinnuloides*. We also thank Iván Valdespino, Christian Lopez, Mireya Correa and the rest of the staff at herbarium PMA for their help with the permits and logistics. The director and staff of Instituto Amazónico de Investigaciones Científicas SINCHI, Bogotá, especially Dairon Cárdenas (herbarium HUA), have been indispensable during our studies across all parts of Colombia with financial and logistical support.

Field trips that contributed to our findings were financed through the German Science Foundation (DFG; grant LE 1826/4) and the research project POPCORN (Using Population genomics, Phylogenetics, and Community Ecology for understanding Radiations in Neotropical mountains) funded by the Swiss National Fund (grant SNF-310030L_146906).

Literature Cited

Barrington, D. S. 1978. A revision of the genus *Trichipteris*. Contributions from the Gray Herbarium of Harvard University 208:3-93.

Christ, H. 1901. Filices. In: Pittier, H. (ed.) Primitiae Florae Costaricensis 3(1):1–62.

Christ, H. 1906. Primitiae Florae Costaricensis, Filices IV. Bulletin de l'Herbier Boissier, sér, 2:279–288.

Hooker, W. J. and J. G. Baker. 1868. *Synopsis Filicum*. R. Hardwicke, London.

Kao, T. T., K. M. Pryer, M. D. Turner, R. A. White, and P.Korall. 2015. Origins of the endemic scaly tree ferns on the Galápagos and Cocos Islands. International Journal of Plant Sciences 176:869–879.

Kuhn, M. 1869. Reliquiae Mettenianae. Linnaea 36:41–169

Lehnert, M. 2011. Species of *Cyathea* in America related to the western Pacific species *C. decurrens*. Phytotaxa 26:39–59.

Lehnert, M. and A. Weigand, 2017. A synopsis of the Neotropical species of *Cyathea* (Cyatheaceae; Polypodiopsida) with bipinnate fronds. Brittonia 69:71–90. https://doi.org/10.1007/s12228-016-9445-1

Lellinger, D. B. 2002. A modern multilingual glossary for taxonomic pteridology. Pteridologia 3:1–264.

Loiseau, O., A. Weigand, S. Noben, J. Rolland, D. Silvestro, M. Kessler, M., Lehnert, and N. Salamin. 2020. Slowly but surely: gradual diversification and phenotypic evolution in the hyperdiverse tree fern family Cyatheaceae. Annals of Botany 125:93–103.

Maxon, W. R. 1911. On the identity of *Cyathea multiflora*, type of the genus *Hemitelia* R. Br. Bulletin of the Torrey Botanical Club 38:545–550.

Maxon, W. R. 1912. The tree ferns of North America. The Smithsonian Report for 1911 (Vol. 2120):463–491+15 pl.

Moran, R. C. 1991. Eight new species of tree ferns (*Cyathea*, Cyatheaceae) from the American tropics and three new combinations. Novon 1:88–104.

Moran, R. C. 1995. Five new species and two new combinations of ferns (Polypodiopsida) from Ecuador. Nordic Journal of Botany 15:49–58.

Pérez-Escobar, O. A., Lucas, E., Jaramillo, C., Monro, A., Morris, S. K., Bogarín, D., Greer D., Dodsworth, S., Aguilar-Cano, J., Sanchez Meseguer, A. and A.Antonelli. 2019. The origin and diversification of the hyperdiverse flora in the Chocó biogeographic region. Frontiers in Plant Science 10(1328):1–6. https://doi.org/10.3389/fpls.2019.01328

Pittier, H. 1929. Botanical notes on, and descriptions of, new and old species of Venezuelan plants. Journal of the Washington Academy of Sciences 19:175–186.

Rojas-Alvarado, A. F. 2001. Nuevas especies, nombres nuevamente utilizados y nuevas distribuciones en los helechos arborescentes (Filicales: Cyatheaceae) para el Neotrópico. Revista de Biología Tropical 49:453–466.

Rojas-Alvarado, A. F. 2007. Novedades en *Cyathea* (Filicales: Cyatheaceae) para Costa Rica y Panamá. Metodos en Ecología y Sistematica (MES) 2:1–13.

Rojas-Alvarado, A. F. 2008. Short note: New name for one recently described species of *Cyathea*. Metodos en Ecología y Sistematica (MES) 3:43.

Smith, J. E. 1793. Tentamen botanicum de filicum generibus dorsiferarum. Memoires de l'Academie Royale des Sciences (Turin) 5:401–422.

Soria, J. C. P. 1987. El intento de la unidad: la República Federal de Centroamérica, 1823–1840. Mesoamérica, 8(13):3–85.

Stolze, R. G. 1974. A taxonomic revision of the genus *Cnemidaria* (Cyatheaceae). Fieldiana Botany 37:1–98.

Thiers, B. 2019, constantly updated. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. *http://sweetgum. nybg. org/ih.*

Tryon, R. M. 1976. A revision of the genus *Cyathea*. Contributions from the Gray Herbarium of Harvard University 206:19–98.

Véliz Pérez, M. E. and J. M. Vargas Ponce. 2006. *Helechos arborescentes de Guatemala: distribución, diversidad, usos y manejo.* Herbario BIGU, Universidad de San Carlos de Guatemala.

American Fern Journal 111(4):308–326 (2021)
Published on 5 November 2021

Crossing the Divide: An Exploration of Functional Traits in Ferns that Grow Across Terrestrial, Epipetric, and Epiphytic Habitats

Jacob Lewis Watts
Department of Biology, Colgate University, Hamilton, NY USA
jwatts@colgate.edu

James E. Watkins, Jr*
Department of Biology, Colgate University, Hamilton, NY USA
jwatkins@colgate.edu

Abstract.—Plants are characterized by their marked plasticity and ability to alter their functional biology to partition ecological niches. However, there are limits to functional trait exploration especially in complex and stressful habitats. Highly specialized traits may control a species ability to explore within and across habitats. Such may be especially true of epiphytes, whose array of unique traits may constrain their ability to cross establish in epiphytic and terrestrial habitats. In the case of ferns, there are few reported examples of species that can grow across these habitats with regularity. However, this study reports and explores species that exhibit great ecological flexibility growing across a wide range of habitats and growth forms. Specifically, we examine species that grow as 1) terrestrially rooted and epiphytic individuals, 2) nest and non-nest-forming epiphytes; and nest-forming terrestrially rooted individuals, and 3) species that grow as terrestrial, epiphytic, and epipetric individuals. We use natural abundance foliar stable isotope ratios (SIR) of N^{15} and C^{13}, and %N, to explore intraspecific variation in mineral nutrition and water relations across and within niches. Our results reveal the 1) unreported ability of some species to grow across the epiphytic/terrestrial divide, 2) surprising ability of some species to explore these habitats with little to no shift in functional traits; 3) a potentially new function for the nest in nest-forming epiphytes. Finally, our work highlights the need to consider intraspecific trait variation more carefully when studying ferns that occur across a wide range of habitats.

Key Words.—epiphyte, epipetric, niche partitioning, water and nutrient relations, functional biology

As ecosystems evolve and niches fill, organisms are faced with the need for increased functional diversity to more carefully partition their environments. Life form evolution may be one response to niche partitioning and ultimately allows for diverse species coexistence. For example, as angiosperms diversified in the Cretaceous (144 - 65 MYA), they altered global rainfall and climate. This change resulted in the rapid diversification of many plant groups (Heimhofer *et al.*, 2005). Such diversification is thought to have put pressure on niche space and increased the movement of plants from terrestrial ancestors into the epiphytic niche (Schneider *et al.*, 2004; Benzing, 2008; Schuettpelz and Pryer, 2009). Perhaps nowhere is this more obvious today than in wet tropical forests that are structurally and microclimatically complex. Such

* denotes corresponding author

diverse systems create an array of complex habitats for epiphytes to explore and exploit; however, the tropical epiphytic environment is functionally different from the terrestrial environment, the former typically being hotter, brighter, drier, and less nutrient rich than the terrestrial environment (Cardelús and Chazdon, 2005; Cardelús and Mack, 2005; Cardelús *et al.*, 2009). The magnitude of these differences can increase with height in the canopy such that high canopy epiphytes experience a distinct environment when compared to plants rooted in the understory soil. Even a slight increase in height through the understory can result in potentially biologically significant shifts in light and humidity (Cardelús *et al.*, 2009). The contrast between these habitats provides differing selective pressures, and as a result, epiphytic plants are physiologically, and often morphologically unique from their terrestrial colleagues (Rada and Jaimez, 1992; Watkins, Rundel, and Cardelús, 2007; Zotz, 2016; Zhang *et al.*, 2018). Pressures acting across epiphytic and terrestrial may select for highly specialized traits that ultimately lock species into each habitat, reducing their ability to radiate across habitats.

Given the confines of their niche, epiphytes have developed a suite of diverse functional characteristics to enhance water and nutrient acquisition, conservation, and use, including thick, long lasting leaves (Holbrook and Putz, 1996), pendulous vellum coated roots of orchids (Zotz and Winkler, 2013), resource sharing among different ramets of the same rhizome (Lu *et al.*, 2015), symbiotic relationships with insects (Watkins, Cardelús, and Mack, 2008), tank, and nest-forming morphologies that trap leaf litter and water to buffer the plant from drought and nutrient scarcity and inconsistency (Schmidt and Zotz, 2001), and many more fascinating morphologies.

In a review of epiphyte physiological ecology, Zotz and Hietz (2001) concluded that while broad generalizations warrant more research, epiphytes are often limited by water and can be subject to nutrient limitation. Such observations have been supported by more recent work (Lasso and Ackerman 2013; Gora and Lucas 2019) and while these two variables strongly influence epiphyte ecology, this is not the case for all taxa. In a more recent survey on accidental epiphytes, Hoeber and Zotz (2021) found that primarily terrestrial species growing as accidental epiphytes exhibited higher leaf-level nutrient concentrations and showed no evidence of water limitation. For ferns specifically, it has long been known that epiphytic species exhibit myriad adaptations to conserve water. Hietz and Briones (1998) demonstrated that ferns in a wet Mexican cloud forest exhibit increasingly strong water conservation adaptations such as shifts in stomatal traits and increased incidence of CAM higher into the canopy. Campany *et al.* (2021) found that epiphytic ferns exhibit strong drought avoidance adaptations (lower stomatal density, reduced xylem area, thicker leaves, etc.) when compared to terrestrial species. Like sporophytes, fern gametophytes also boast a range of fascinating adaptations to the relatively dry epiphytic environment, including long lifespans and desiccation tolerance (Watkins *et al.*, 2007; Pitterman, Brodersen, and Watkins, 2013). Together, these studies, and many others, reveal significant functional differences between plants growing in epiphytic

and terrestrial habitats, yet suggest that there may be a great deal of plasticity in functional response.

In spite of some of the more predictable trends in functional trait combinations within and across habitats, plants respond in different ways to the same stressors. Thus, it is unlikely that a single trait combination spells success, even in the same habitat. Marks and Lechowicz (2006) used a genetic algorithm to model the survival and growth 34 species of co-occurring tree seedlings and found that interspecific variation in physiological traits was greater than that predicted by variation in the environment, indicating that there is more than one optimal combination of traits for a single environment. Their findings are supported by studies which range from tropical to subarctic environments and show that co-occurring plant species exhibit high trait variation and have settled into different optimal trait combinations for the same environment (Cavender-Bares, Kitajima, and Bazzaz, 2004; Wright *et al.*, 2004; Ackerly and Cornwell, 2007). Such high trait variation commonly occurs within individuals of the same species and is especially apparent if a plant ontogeny is considered (Hietz and Wanek, 2003; Testo and Watkins 2012). Tank-forming bromeliads can drastically change their water and nutrient uptake strategies across ontogeny in response to changing needs: young plants invest more in the capture of atmospheric nutrients while larger plants rely on their tanks for internal nutrient cycling (Schmidt and Zotz, 2001; Zotz, Hietz, and Schmidt, 2001; Laube and Zotz, 2003; Reich *et al.*, 2003). Testo and Watkins (2012) found that the non-nest forming epiphytic fern *Asplenium auritum* showed changes in physiological traits across plant size, shifting from drought tolerance in small plants to drought avoidance in large plants.

In addition to changes that occur with ontogeny, some species exhibit functional trait shifts with changes in life form. For example, hemiepiphytic strangler figs change leaf-level functional traits (Holbrook and Putz, 1996) and some fundamental aspects of their cellular-level physiology (Zhang *et al.*, 2009) as they move from epiphytic to terrestrial individuals. Similar functional trait shifts have been observed between strictly epiphytic and terrestrial orchids (Zhang *et al.* 2015) and ferns (Sulaiman and Cicuzza, 2021). Excluding the relatively rare examples of hemiepiphytic species, few fern species have the ability to grow in both habitats. Watkins *et al.* (2006) found only a single species of *Elaphoglossum* out of 264 fern species across 60 genera that could grow as both a high canopy exposed epiphytic and as understory terrestrial individuals on the Barva Transect in Costa Rica. A similar paucity of reciprocal occurrence has been reported in the series of papers by Kluge and Kessler (2007, 2011, and references therein) who completed transects on the same elevational gradient. There are many reports of fern species occurring in both epiphytic and terrestrial habitats and obviously these studies do not say cross occurrence never occurs, yet few fern species can be found in the extremes, i.e., high canopy or highly exposed epiphytic conditions and growing in the mineral soil. Cases where species cross these boundaries, for example primarily understory epiphytes apparently growing in understory soil, are usually facilitated by habitat heterogeneity and the occurrence of rocks and/or

rotting logs (Canestraro, Moran, and Watkins, 2014). Much more work must be done to understand mechanistic parameters and to quantify the extent to which fern species actually exhibit reciprocal establishment across these habitats. Reports on floristic assemblages and keys rarely distinguish between occurrence and establishment and frequently confuse accidental occurrences with the more typical state of species. All of this taken together suggests that shifts in functional traits, changes in physiology, and general rarity of individual species that can explore epiphytic and terrestrial habitats suggest habitat fidelity.

This paper aims to explore inter and intraspecific variation in physiological traits of ferns across an array of niches and life forms *in situ*. Specifically, we examine percent nitrogen (%N), the ^{15}N:^{14}N stable isotopic ratio (SIR) ($\delta^{15}N$), and ^{13}C:^{12}C SIR ($\delta^{13}C$) of: 1) two species of the genus *Elaphoglossum*, E. *eximium* (Mett.) Christ and *E. erinaceum* T. Moore, that grow across terrestrial, epipetric, and epiphytic niches and 2) two species in the Polypodiaceae that grow as nest-forming epiphytes and terrestrials, *Niphidium crassifolium* (L.) Lellinger and *Serpocaulon fraxinifolium* (Jacq. A.R.Sm.) as both epiphytic and terrestrial plants. We chose to examine these traits because they are well studied and related to water and nutrient relations, two aspects that are likely to be critical to plants growing on such disparate substrates such as soil, rocks, and trees. Given the complex nature of epiphyte ecophysiology and the differences between and even within co-occurring species, we predict that each species will exhibit a unique response to growth across different niches: epiphytic, epipetric, and terrestrial.

Materials and Methods

Study sites.—Samples were collected from Las Cruces Biological Station (8° 47′ 7” N, 82° 57′ 32” W) in Puntarenas Province, Costa Rica and along the river that passes through the Savegre Lodge property (9° 33′ 12” N, 83° 48′ 23” W) in San José Province, Costa Rica (permit nos. No PI-R-072-2018 to J. E. Watkins Jr). The Las Cruces Biological Station is in a mid-elevation (1000 m elevation) tropical wet forest that has a mean total annual rainfall typically around 3500 mm, with wet seasons in May and September-October, and a pronounced dry season in December-March. January is the driest month during which only 50 mm of rainfall occur on average (www.ots.ac.cr). The collection site was characterized by high light and low canopy cover due to its juxtaposition with young secondary rainforest.

The Savegre Lodge property is in a premontane (2200 m elevation) wet cloud forest that has a mean total annual rainfall of 3600 mm, with wet seasons in May and September-October, and a dry season in December-March. February receives only 70 mm of rainfall (en.climate-data.org). The study site was characterized by low light, high humidity, with evidence of flooding during the wet season.

A total of 101 samples from four epiphytic fern species across three genera were collected at two study sites. Sampling was equal with approximately 10

samples per treatment per species. Primarily epiphytic species were observed and collected as 1) low trunk, non-nest forming epiphytes (within 2.5 m of the soil), 2) low trunk nest-forming epiphytes, 3) terrestrially rooted plants (with and without a nest), and as 4) epipetric (growing on rocks) plants. Species collected at Las Cruces include *Niphidium crassifolium* (epiphytic, nest-forming epiphytic, and terrestrial), and *Serpocaulon fraxinifolium* (epiphytic and terrestrial) (Fig. 1). Species collected at Savegre include *Elaphoglossum eximium* and *Elaphoglossum erinaceum*. Both *Elaphoglossum* species lie within the *E. subulata* clade (Rouhan *et al.* 2004) and were collected as epiphytic, epipetric, and terrestrial individuals (Fig. 2).

A word on isotopes.—There is a dizzying array of plant functional traits that have been cited and measured across a remarkable diversity of studies. In fact, the TRY Plant Trait Database now lists over 2,091 separate traits from 280,000 plant taxa (Kattge *et al.* 2020). Of these 2,091 traits, there is little consensus as to the most important traits one should use. Much of this is context dependent and often based on what the investigator has the capacity to carry out. Nitrogen content is related to metabolism and among other things, there is typically an increased capacity for photosynthesis with more %N. Dawson *et al.* (2002) wrote an excellent review on the use of stable isotopes in ecology useful in understanding the use of isotopes. The application of stable isotopes is largely based on the idea that normal metabolic reactions abhor heavy isotopes and "avoid" them in a process known as biological isotope fractionation. For example, carbon exists as three isotopes C^{12}, C^{13}, C^{14} that vary in their overall concentration in our atmosphere with C^{12} being the most abundant (approximately 99% of atmospheric C) and the radioactive C^{14}, thankfully, being the rarest (Boutton, 1991). When we think of photosynthesis, CO_2 is taken in through the stomata and enters the dark reactions through the catalyzing nature of RuBisCO (Ribulose-1,5-bisphosphate carboxylase-oxygenase). RuBisCO has a natural affinity for the lighter isotope C^{12} and will discriminate against C^{13} and C^{14}. This act of discrimination allows scientists to evaluate certain aspects of the water relations of a plant (Farquhar, Ehleringer, and Hubick, 1989). Typically, internal leaf spaces become filled with CO_2 gas and if the stomata are open, a larger proportion of $C^{13}O_2$ and $C^{14}O_2$ diffuses from the leaf as RuBisCO reacts more readily with $C^{12}O_2$. However, if a plant must close its stomata to conserve water, no new CO_2 gas can enter, and RuBisCO will continue to preferentially deplete $C^{12}O_2$ in the substomatal cavity. This increases the internal ratio of $C^{13}O_2$ to $C^{12}O_2$ eventually causing the plant to use more $C^{13}O_2$ and $C^{14}O_2$. In this case, the leaf will become enriched in the heavier isotopes (compared to a plant with open stomata and high stomatal conductance) and in general terms, one can assume that a leaf with an enriched C isotope signal may close its stomata (or have lower stomatal conductance) more often than a less water use efficient leaf. Thus, a plant with a higher $\delta^{13}C$ SIR has greater water use efficiency (WUE). Nitrogen isotopes are perhaps more difficult to summarize as many biological processes play a part in altering the ratio of N isotopes; however, one interpretation of a plant's natural N^{15} abundance is nitrogen source. As total

Fig. 1. Las Cruces species *Niphidium crassifolium* (A-C) and *Serpocaulon fraxinifolium* (D-E) growing across epiphytic and terrestrial habitats. *N. crassifolium* develops a nest over time as its fronds get wider and dead fronds accumulate at the bottom of the plant. The nest morphology may allow for the capture of water and leaf litter. *S. fraxinifolium* has a long creeping rhizome. Photo credit: Robbin C. Moran, picture (B).

Fig. 2. Savegre Lodge species *Elaphoglossum eximium* (A-C) and *Elaphoglossum erinaceum* (D-F) occurring abundantly on soil (A&D), rocks (B&E), and trees (C&F).

nitrogen (a combination of the N^{14} and N^{15} isotopes) passes through an ecosystem, metabolism again discriminates against the heavier isotope. So, a plant that obtains nitrogen from N-fixing bacteria, which convert N_2 directly from the atmosphere, will be depleted in N^{15} relative to a plant that absorbs nitrogen from decaying leaf litter. Nitrogen found in leaf litter has undergone more biological fractionation. Interpretation of $\delta^{15}N$ SIR data can be controversial, but in this paper, we use $\delta^{15}N$ SIR data as a possible indicator of where plants obtain nitrogen.

Sample preparation for isotopic and nutrient analyses.—Air dried field samples were taken to the lab and oven dried at 60 °C, pulverized into a fine powder with a Wiley Mill (Thomas Scientific Model 3383-L10), and weighed and rolled inside tin capsules (5 by 9mm Costech pressed tin capsules).

Prepared samples were analyzed for %N and δ^{15}N and δ^{13}C SIRs at the Cornell Stable Isotope Laboratory (COIL) (Ithaca, NY, USA) using a Finnigan Matt Delta Plus IRMS. Leaf isotope numerical values are expressed in delta notation (δ) and are relative to the standard PDB (Pee Dee Belemnite) and air, for both C and N.

Statistical Analysis.—Our data met the normality assumptions of parametric statistical tests as per Shapiro-Wilk tests for each variable (%N, δ^{15}N, and δ^{13}C SIRs) by site ($\alpha = 0.05$). To avoid the confounding effects of site differences, comparisons were never made across sites. Comparisons between species were only made with closely related species – *Elaphoglossum eximium* and *E. erinaceum* – growing in the same habitat. When two groups were compared, two-sample t-tests were used to determine if groups exhibited significant differences ($\alpha = 0.05$). If variances between groups were unequal via a Welch F-test, then Welch's two-sample t-test (unequal variance) was performed instead. When three groups were compared, analysis of variance (ANOVA) followed by post-hoc Tukey Honest Significant Difference tests were used to determine significant differences among groups ($\alpha = 0.05$). Comparisons include: 1) two-sample t-test between terrestrial and epiphytic *S. fraxinifolium*; 2) analysis of variance between epiphytic, epiphytic nest-forming, and terrestrial *N. crassifolium*; 3) two-sample t-test between *E. eximium* and *E. erinaceum* within habitat; 4) analysis of variance between epiphytic, epipetric, and terrestrial individuals of *E. eximium* and *E. erinaceum*, treated separately. All statistical analyses were performed in R version 4.0.2: packages 'base' (R Core Team, 2020) and 'dplyr' (Wickham *et al.*, 2020). All graphs were plotted using 'ggplot2,' (Wickham, 2016) 'ggpubr,' (Kassambara, 2020) 'ggsignif,' (Ahlmann-Eltze, 2019) and 'rstatix' (Kassambara, 2020) packages.

Results

Global results.—Across all 101 samples taken, plants exhibited a wide range of %N, δ^{15}N, and δ^{13}C SIR values. Sampled plants exhibited %N values ranging from 0.8% to 2.7% with a mean of 1.8%. δ^{15}N values ranged from highly depleted (less processed) (-5.9) to enriched (more processed) (2.3) with a global mean value of -1.7. δ^{13}C values ranged from enriched (high WUE) (-28.9) to depleted (low WUE) (-35.8) and averaged -32.7 across all samples.

Serpocaulon fraxinifolium grew abundantly as an epiphyte in the low canopy (Fig. 1D) and scattered as terrestrial individuals along the forest floor (Fig. 1E). Morphologically, the species did not differ obviously between life forms, except that the rhizome grew horizontally across the soil when found as a terrestrially rooted plant and vertically up tree bark when epiphytic. Curiously, we found no significant differences between the epiphytic and terrestrial individuals in either %N ($t_{10.5} = -0.256$, $p = 0.80$), δ^{15}N SIR ($t_{10.9} = -0.873$, $p = 0.40$), or δ^{13}C SIR ($t_{11.9} = 0.437$, p-value = 0.67) (Fig. 3A-C).

Mature *Niphidium crassifolium* (Fig. 1A-C) individuals were found growing abundantly in the understory as large plants with well-developed nests. Immature individuals (2-6 fronds, Fig. 1A) were also found as epiphytes, but

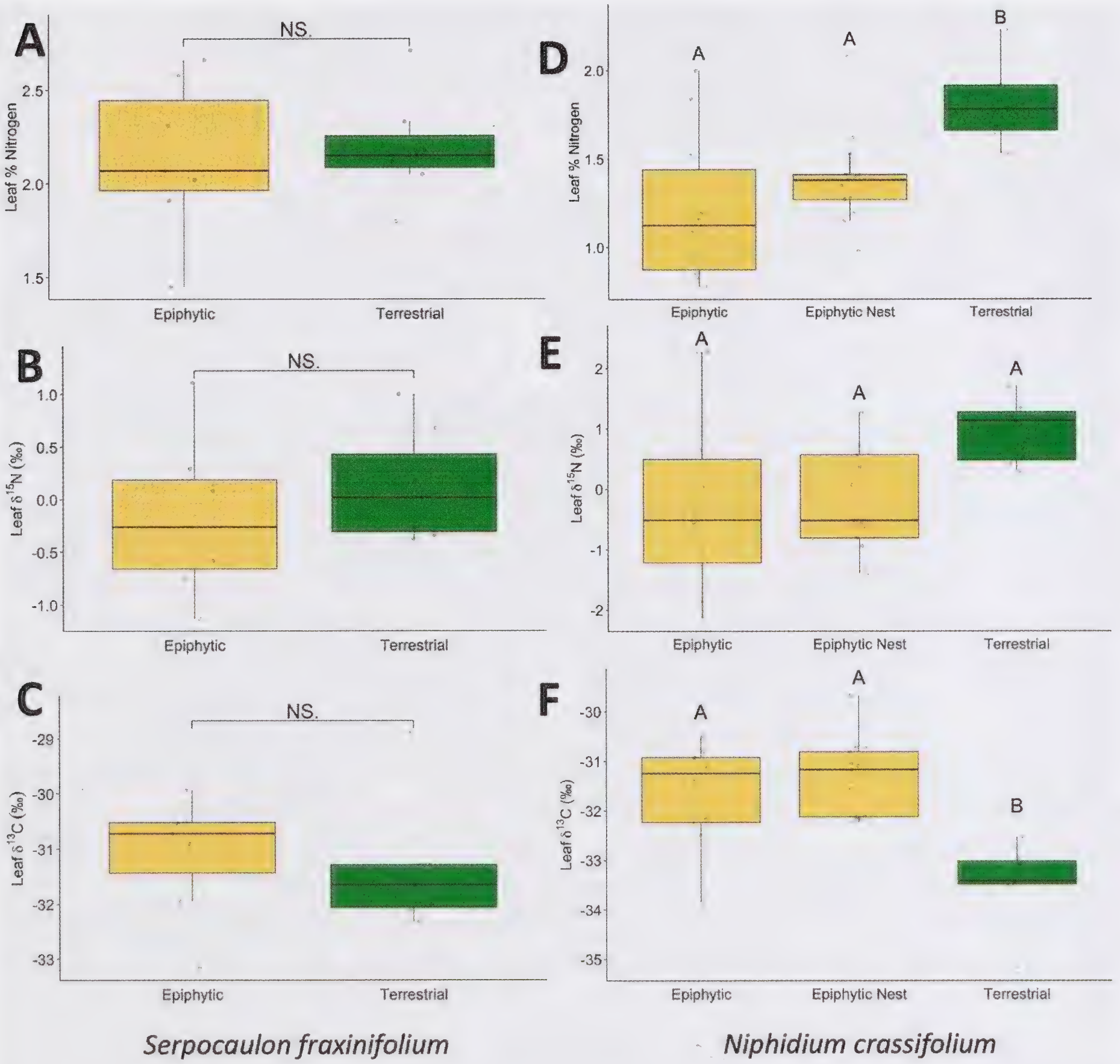

Fig. 3. Boxplots of trait values for Las Cruces species *Serpocaulon fraxinifolium* (A-C) and *Niphidium crassifolium* (D-F) compared across epiphytic and terrestrial habitats *in situ*. Boxes represent the interquartile range and lines represent the median. Whiskers represent the highest and lowest values within 1.5 times the interquartile range. Each individual sample is denoted by grey dots. Significant differences are denoted by NS., *, **, *** corresponding to >0.05, <0.05, <.01, and <.001 p-values respectively as determined by T-tests. Uppercase letters denote significant differences determined from ANOVA and post hoc Tukey tests ($p < 0.05$). Colors correspond to habitat (yellow = epiphytic, green = terrestrial).

lacked a fully-formed nest morphology (Fig. 1B-C). Fully mature, fertile, and seemingly healthy ferns growing rooted in the mineral soil were also observed. At this site, we never observed young plants recruiting on the soil, so we assumed that these terrestrial plants represented fallen individuals. In all sampled cases, these plants were solidly rooted in the mineral soil, having fallen long ago. Terrestrial *N. crassifolium* were relatively abundant, though not as abundant as epiphytic *N. crassifolium*. Terrestrially rooted *N. crassifolium* had a higher %N than both epiphytic life forms ($F_{2,27} = 7.08$, p

< 0.01): nest epiphytic ($p = 0.03$), and non-nest epiphytic ($p < 0.01$) (Fig. 3D). $\delta^{15}N$ SIRs did not differ among life forms ($F_{2,27} = 3.005$, $p = 0.06$), while $\delta^{13}C$ SIRs did ($F_{2,27} = 13.47$, $p < 0.001$) (Fig. 3F). Terrestrially rooted *N. crassifolium* had more depleted $\delta^{13}C$ values (less WUE) than conspecific non-nest epiphytes ($p < 0.001$) and nest epiphytes ($p < 0.001$) (Fig. 3F).

Elaphoglossum eximium and *Elaphoglossum erinaceum* grew abundantly in the low canopy on the tree trunks (Fig. 2C&F), on large and small boulders (Fig. 2B&E), and rooted in the rocky mineral soil (Fig. 2A&D). Individuals were collected along the Rio Savegre at the bottom of a ravine within 10-20 m of the river side. The area was wet and showed evidence of recent flooding such as the presence of silt covering the lower trunks of trees. The river is known to flood this ravine frequently (Felipe Chacón Vargas pers. comm.) %N varied by life form ($F_{2,25} = 7.39$, $p < 0.01$), with epipetric *E. erinaceum* having greater %N compared to conspecific epiphytic individuals ($p < 0.01$) with terrestrial individuals exhibiting intermediate %N to epipetrics ($p = 0.18$) and epiphytes ($p = 0.14$) (Fig. 4A). Surprisingly, *E. erinaceum* $\delta^{15}N$ SIRs did not respond to different growth substrates ($F_{2,25} = 0.116$, $p = 0.89$) (Fig. 4B); while $\delta^{13}C$ SIRs did differ among substrates ($F_{2,25} = 4.26$; $p = 0.03$). According to a post hoc Tukey, epiphytic *E. erinaceum* individuals were more water use efficient (more enriched in C^{13}) than terrestrially rooted individuals ($p = 0.02$), but did not differ from epipetric individuals ($p = 0.30$). Epipetric and terrestrial individuals did not differ from one another ($p = 0.44$) (Fig. 4C).

Elaphoglossum eximium exhibited no response to substrate in either leaf tissue %N ($F_{2,26} = 1.74$, $p = 0.20$), or $\delta^{13}C$ SIR ($F_{2,26} = 1.518$, $p = 0.24$) (Fig. 4A&C). However, leaf tissue $\delta^{15}N$ SIR was correlated by life form in *E. eximium* ($F_{2,26} = 4.587$, $p = 0.02$). Epipetric individuals utilized less processed nitrogen than epiphytic individuals ($p = 0.02$), but were not different from terrestrial individuals ($p = 0.39$). Terrestrial and epiphytic individuals also did not differ ($p = 0.18$) (Fig. 4B).

We also tested for differences between these two closely related species growing on similar substrates to investigate the possibility of niche partitioning in nutrient and water acquisition and use. Using Welch's t-tests, no differences in %N were detected between *E. eximium* and *E. erinaceum* growing on trees ($t_{16.1} = 0.656$, $p = 0.64$), rocks ($t_{12.5} = -2.38$, $p = 0.10$), or soil ($t_{18} = 1.02$, $p = 0.64$) (Fig. 4A). *E. erinaceum* utilized less processed nitrogen than *E. eximium* while growing on trees ($t_{17.1} = -3.40$, $p = 0.01$), but the species were not different while growing on rocks ($t_{12.2} = -0.297$, $p = 0.77$) or soil ($t_{9.5} = -2.09$, $p = 0.13$) (Fig. 4B). Interestingly, *E. eximium* had at least marginally ($p < 0.1$) higher WUE than *E. erinaceum* across all substrates: trees ($t_{10.4} = 1.82$, $p = 0.01$), rocks ($t_{13.2} = 2.24$, $p = 0.09$), and soil ($t_{13.4} = 3.05$, $p = 0.03$) (Fig. 4C).

Discussion

Epiphytic ferns are often presented as growing at their physiological limits, surviving on the edge, disconnected from the soil, and in highly competitive

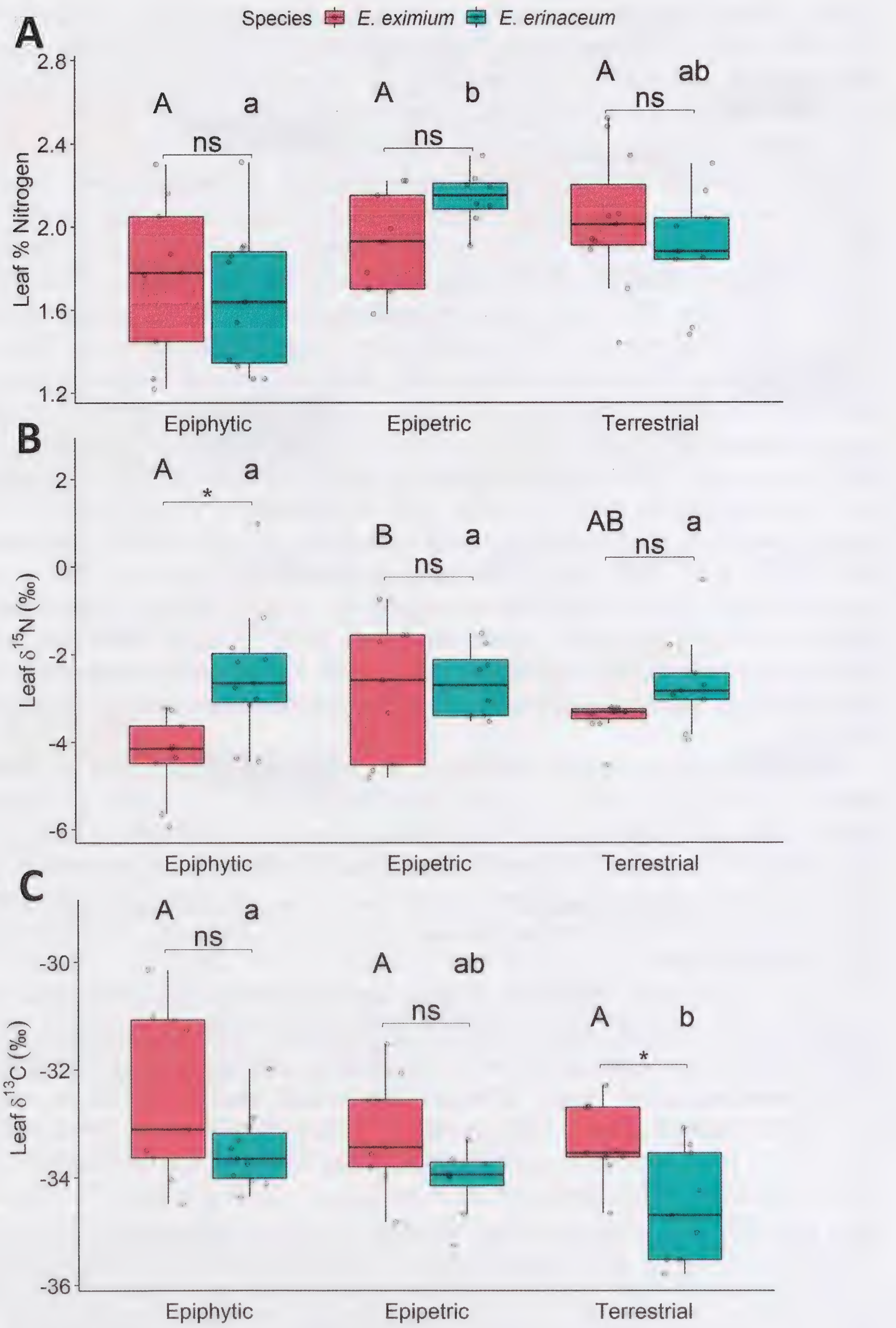

Fig. 4. Boxplots of %N (A), $\delta^{15}N$ (B), or $\delta^{13}C$ SIRs (C) for Savegre species *Elaphoglossum eximium* and *Elaphoglossum erinaceum*. Boxes represent the interquartile range and lines represent the median. Whiskers represent the highest and lowest values within 1.5 times the interquartile range. Each individual sample is denoted by grey dots. Significant differences are denoted by NS., *, **, *** corresponding to >0.05, <0.05, <.01, and <.001 p-values respectively as determined by T-tests. Uppercase and lowercase letters denote significant differences determined from ANOVA and post hoc Tukey tests performed across habitats and within species ($p < 0.05$). Colors correspond to species.

environments (Hsu *et al.*, 2012; Ding *et al.*, 2016; Santiago *et al.*, 2017). In stressful habitats, plants have a limited range of functional trait values available to them. For this reason, epiphytes are often treated as a single functional group, adapted under a similar set of limitations that produce a predictable set of morphological and physiological adaptations (Stewart *et al.*, 1995; Watkins, Rundel, and Cardelús, 2007; Mardegan *et al.*, 2011; Nitta, Watkins, Jr., and Davis, 2020). While such classifications often come from large comparative studies and have reasonable applications when comparing across habitats, they may be overly simplistic. This concept is not entirely new as some studies have suggested that there can be significant *intra*specific variation in epiphyte functional traits and such variation may surpass interspecific variation reported in some species (Petter *et al.*, 2015; Hurtado *et al.*, 2020); however few studies have carefully examined such traits in tropical epiphytic ferns. The goal of the current study is to take a closer look at inter and intraspecific trait variation in fern taxa that can grow across multiple habitats.

At the Savegre site, *Elaphoglossum eximium* and *Elaphoglossum erinaceum*, both species of the *Elaphoglossum subulata* (subulate scales) clade, grow in close proximity often intermixed on soil, rocks, and trees (Fig. 2). Morphologically, the two species are similar, and they inhabit similar niches, however their N content and $\delta^{15}N$ SIR can often differ, even when growing on the same substrate (Fig. 4B-C). The range of intraspecific and interspecific trait values suggests that the two co-occurring *Elaphoglossum* species are highly plastic and simultaneously limited by some resources and unaffected by discrepancies in others, depending on the substrate. The work of Cardelús and Mack (2009) on epiphyte mineral nutrition produced similar results: inter- and intraspecific variation in $\delta^{15}N$ SIR across an elevational gradient was high and did not correlate with differences in the mineral nutrition of the host tree or elevation, leading the authors to conclude that resource partitioning among epiphytes may contribute to high diversity in the epiphytic niche. Marks and Lechowicz (2006) describe a similar phenomenon among temperate tree species: trait values reach different optimums within a relatively homogenous niche which suggests that there is not a single combination of traits that spells success for any given habitat. Corresponding patterns have been found in non-ferns and Albert *et al.* (2011) caution that intraspecific trait variation is often incorrectly ignored in many analyses and should be incorporated more often.

The charismatic nest forming ferns characteristic of the paleotropics are nearly absent in the neotropics and those present never quite reach the size and ecological importance of old world *Asplenium* and *Platycerium*. *Niphidium crassifolium*, a neotropical species, comes in a distant third with its ability to form moderately large nests, especially in older plants (Fig. 1B). We were particularly interested in this species as 1) we suspected that nest-forming plants would be physiologically different from non-nest plants and 2) at Las Cruces, it is not uncommon to find large healthy plants firmly rooted and thriving in terrestrial mineral soil. This provided us with yet another opportunity to evaluate an epiphytic/terrestrial species with the potential

addition of a nest influence. Surprisingly, we found no differences between young, non-nest forming epiphytic individuals of *Niphidium crassifolium* and older, epiphytic nest-forming individuals (Fig. 3D-F). This was quite unexpected as the non-nest forming plants were significantly smaller and likely younger than those with litter-trapping nests. At this site, Las Cruces, it was only the large plants that formed noticeable nests. Nests can typically provide benefits to epiphytes and act to store water and enhance nutrient capture (Benzing, 1989; Watkins *et al.*, 2008; Jian *et al.*, 2013). While similar but not functionally equivalent to nests, Hietz and Wanek (2003) found bromeliad species that shift from atmospheric to tank-forming morphologies exhibited a positive relationship between $\delta^{15}N$ and a negative relationship between $\delta^{13}C$ SIRs and plant size, indicating changes in N source and WUE with size, a finding reinforced by Reich *et al.* (2003). Testo and Watkins (2012) found similar size mediated changes in physiology in the non-nest forming fern *Asplenium auritum* Sw. There is evidence that both size and nest formation can influence physiology, yet we did not detect this in *N. crassifolium*.

One particularly intriguing aspect of the biology of *Niphidium crassifolium* at this site was its ability to survive and flourish on the forest floor. We discovered dozens of large plants rooted in the mineral soil and in all cases, these plants were quite large. When we compared these rooted plants to epiphytic ones, they were significantly less water use efficient (WUE), had higher foliar %N, and generally, although not significantly, utilized more highly processed N sources (Fig. 3D-F). Both patterns reflect what is typically expected in terrestrial/epiphytic comparisons. Even though these plants were rooted in the soil, their nests were still filled with fallen leaves, twigs, and other organic matter, all of which likely supplement the nitrogen and water relations of these plants. It was notable that we found no small plants growing on soil. From this, we believe that these terrestrial plants represent fallen individuals and not plants that originally established on the forest floor. In most cases, fallen epiphytic ferns that land on soil rarely survive long and typically exhibit rapid decline (J.E. Watkins pers. obs.). Yet, *N. crassifolium* frequently seems to thrive in such conditions. While most have viewed nests as an adaptation for nutrient capture and water storage (e.g., Freiberg, 1997; Turner and Foster, 2006; Suhaimi and Cicuzza, 2020), epiphytes eventually fall, and it is possible that nests serve a role in the survival and terrestrial establishment of these plants perhaps by buffering them from changes in their new microenvironment. We have also observed the phenomenon in tropical forests in Australia, where is it not uncommon to find bird's nest *Asplenium* growing on the forest floor.

Perhaps one of the most unexpected results of this work was our failure to detect a consistent difference between soil rooted and epiphytic plants of *Serpocaulon fraxinifolium*. This species is a somewhat weedy epiphyte with a green, creeping rhizome that is abundant in secondary forests. Plants did not differ with life form in any of the variables tested (Fig. 3A-C). In all cases, we carefully traced the rhizomes to their point of rooted origin and were sure that

we sampled from epiphytic or terrestrial individuals and not simply from scrambling plants. This could suggest that 1) there is not an elevated level of water stress or shift in N source associated with these niches, or that 2) *S. fraxinifolium* is particularly flexible and has optimized other traits that we did not measure to offset niche differences, or that 3) unlike terrestrial and canopy habitats, the biotic and abiotic differences between the low trunk epiphytic and terrestrial niches may not be distinct enough to produce more obvious differences at this site.

The epiphytic niche is unusual in many ways and is characterized by nutrient and water poverty, comparatively higher temperatures, and brighter light than terrestrial habitats (Cardelus and Watkins 2007; Nitta, Watkins, and Davis, 2020). Combined, these conditions select for a complex set of traits in species that inhabit the epiphytic niche of tropical rainforests. It is for this reason that few species can live equally as both true epiphytic and terrestrial individuals. Overall, our paper demonstrates the dynamic nature of some taxa as they explore these habitats and is one of the few to carefully examine individual species that can cross the epiphyte/terrestrial divide. Some species like those we studied in *Elaphoglossum* and *Niphidium* reflect many of the expected functional traits reported from several studies cited above. While intraspecific functional trait exploration is limited to some degree in our data, what is notable about these taxa is their flexibility to grow in both habitats and to take on functional traits that reflect the different selective pressures of each growing condition. Perhaps more surprising is *Serpocaulon,* which, at this site, was able to grow in both habitats with little evidence of trait shifts. However, it is likely that this species exhibits other responses to these disparate environments and our ability to detect these was limited by the traits we chose. In spite of this possibility, it is noteworthy that this taxon has consistent nitrogen content and isotopic ratios across habitats, as these traits typically differ with habitat.

Taken together, the results of this study suggest that the epiphytic niche is not necessarily a stressful environment as some species can cross establish with few physiological consequences; a confirmation of the hypothesis put forth by Zotz and Heitz (2001). This niche is partitioned by different species, functional groups, and even individual plants in myriad ways, creating the conditions for hyperdiversity in a liminal habitat (Woods, Cardelús, and DeWalt, 2015; Nitta, Watkins, and Davis, 2020). Though cross establishment of ferns between epiphytic and terrestrial habitats may be uncommon, especially in seasonal lowland tropical forests (Canestraro, Moran, and Watkins, 2014), our study suggests that species found in both habitats can sometimes exhibit few measurable physiological differences between habitats, as in the case of *S. fraxinifolium*, or exhibit marked plasticity but still thrive across habitats as in the case of *Elaphoglossum* spp. Our results may have implications in understanding the functional evolution of fern epiphytes. While some have implicated the "hemiepiphytic bridge" hypothesis to explain the evolution of vascular epiphytes from terrestrial ancestors (Lagomarsino, Grusz, and Moran, 2012; Watts, Moran, and Watkins, 2019), or of hemiepiphytes from epiphytic

and climbing ancestors (Testo and Sundue, 2014), our results suggest that in some lineages, radiation into the canopy may have been possible through, 1) an understory-epiphyte and/or 2) an epipetric bridge. This is perhaps especially true in wet, dark understories and less seasonal forests where the physiological barriers to cross establishment may not be as great as movement directly into the high canopy. Our data are also intriguing in their support of the potential role of the epiphytic nest in the survival and establishment of fallen epiphytes. It is possible that, in capturing fallen organic matter, nests create their own soil and have roots pre-disposed to absorbing nutrients from the mineral soil.

An important and unresolved question of this work is that of establishment. We believe it unlikely that *Niphidium* establishes on the forest floor, but we cannot say the same of *Serpocaulon*. Further investigation of the gametophyte and young sporophyte ecology of these species (and of tropical ferns in general) is required before more clear determinations can be made. However, it is clear from the sheer numbers that *Elaphoglossum eximium* and *E. erinaceum* establish across the three habitats we observed. Other biological interactions at the spore and gametophyte level such as gametophyte physiology, form, reproductive ecology, gametophyte interactions with bryophytes, etc. may limit the cross establishment of epiphytic and terrestrial ferns (Watkins and Moran, 2019; Harrington and Watts, 2021). However, more research must be done as an increasing number of studies have recently demonstrated that gametophytes often extend beyond the range of their sporophyte counterparts, possibly to explore novel habitats (Farrar, 1967; Ebihara, Farrar, and Ito, 2008; Kuo *et al.*, 2017, reviewed in Pinson *et al.*, 2017). Thus, in order to fully understand the evolution of niche partitioning across and within habitats, gametophyte ecology should not be overlooked. Overall, our study encourages us to rethink the traditional notion of the exclusive epiphytic niche and suggests that, in light of a growing body of literature, a more nuanced, species/functional group perspective be taken in future studies on epiphytes.

Acknowledgements

We would like to thank Fernando Matos and Robbin C. Moran for species identification in the tricky, 700+ species genus *Elaphoglossum*. We would also like to thank the fern community for their continued passion for and support of the study of ferns and those Pteridologists that undertake it like ourselves. Finally, we thank two anonymous reviewers of this manuscript for their helpful comments and the editors of the American Fern Journal for careful handling of this manuscript.

Literature Cited

Ackerly, D. D. and W. K. Cornwell. 2007. A trait-based approach to community assembly: partitioning of species trait values into within-and among-community components. Ecology Letters 10:135–145.

Ahlmann-Eltze, C. 2019. ggsignif: Significance Brackets for 'ggplot2'. R package version 0.6.0.

Albert, C. H., F. Grassein, F. M. Schurr, G. Vieilledent, and C. Violle. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? Perspectives in Plant Ecology, Evolution, and Systematics 13:217–225.

Benzing, D. H. 1989. The mineral nutrition of epiphytes. Pp. 167–199, *in* Vascular plants as epiphytes. Ecological Studies 76. Switzerland: Springer International Publishing.

Benzing, D. H. 2008. *Vascular epiphytes: general biology and related biota.* Cambridge University Press.

Boutton, T.W., D. C. Coleman, and B. Fry (eds.). 1991. Stable carbon isotope ratios of natural materials: 2 Atmospheric, terrestrial, marine, and freshwater environments. United States: Academic Press, Inc.

Campany, C., J. Pittermann, A. Baer, H. Holmlund, E. Schuettpelz, K. Mehltreter, and J. E. Watkins Jr. 2021. Leaf water relations in epiphytic ferns are driven by drought avoidance rather than tolerance mechanisms. 44:1741–1755.

Canestraro, B.K., R.C. Moran, and J.E. Watkins, Jr. 2014. Reproductive and physiological ecology of climbing and terrestrial *Polybotrya* (Dryopteridaceae) at the La Selva Biological Station, Costa Rica. International Journal of Plant Sciences 175:432–441.

Cardelús, C. L. and R. L. Chazdon. 2005. Inner-crown Microenvironments of Two Emergent Tree Species in a Lowland Wet Forest. Biotropica 37:238–244.

Cardelús, C. L., M. C. Mack, C. Woods, J. DeMarco, and K. K. Treseder. 2009. The influence of tree species on canopy soil nutrient status in a tropical lowland wet forest in Costa Rica. Plant and Soil 318:47–61.

Cardelús, C. L., and M. C. Mack. 2010. The nutrient status of epiphytes and their host trees along an elevational gradient in Costa Rica. Plant Ecology 207:25–37.

Cavender-Bares, J., K. Kitajima, and F. A. Bazzaz. 2004. Multiple Trait Associations in Relation to Habitat Differentiation Among 17 Floridian Oak Species. Ecological Monographs 74:635–662.

Dawson, T. E., S. Mambelli, A. H. Plamboeck, P. H. Templer, and K. P. Tu. 2002. Stable isotopes in plant ecology. Annual Review of Ecology and Systematics 33:507–559.

Ding, Y., G. Liu, R. Zang, J. Zhang, X. Lu, and J. Huang. 2016. Distribution of vascular epiphytes along a tropical elevational gradient: disentangling abiotic and biotic determinants. Scientific Reports 6:1–11.

Ebihara, A., D. R. Farrar, and M. Ito. 2008. The sporophyte-less filmy fern of eastern North America *Trichomanes intricatum* (Hymenophyllaceae) has the chloroplast genome of an Asian species. American Journal of Botany 95:1645–1651.

Farrar, D. R. 1967. Gametophytes of four tropical fern genera reproducing independently of their sporophytes in the southern Appalachians. Science 155:1266–1267.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Biology 40:503–537.

Freiberg, M. 1997. Spatial and temporal pattern of temperature and humidity of a tropical premontane rain forest tree in Costa Rica. Selbyana 18:77–84.

Gora, E.M. and J.M. Lucas. 2019. Dispersal and nutrient limitations of decomposition above the forest floor: Evidence from experimental manipulations of epiphytes and macronutrients. Functional Ecology 33:2417–2429.

Harrington, A. D., and J. L. Watts. 2021. Low Trunk Epiphytic Fern Gametophyte and Sporophyte Occurrence Is Influenced by Moss Height and Density in a Costa Rican Lowland Tropical Rainforest. International Journal of Plant Sciences 182:286–294.

Heimhofer, U., P. A. Hochuli, S. Burla, J. M. L. Dinis, and H. Weissert. 2005. Timing of Early Cretaceous angiosperm diversification and possible links to major paleoenvironmental change. Geology 33:141–144.

Hietz, P., and O. Briones. 1998. Correlation between water relations and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. Oecologia 114:305–316.

Hietz, P., W. Wanek, and M. Popp. 1999. Stable isotopic composition of carbon and nitrogen and nitrogen content in vascular epiphytes along an altitudinal transect. Plant, Cell & Environment 22:1435–1443.

Hietz, P., and W. Wanek. 2003. Size-Dependent Variation of Carbon and Nitrogen Isotope Abundances in Epiphytic Bromeliads. Plant Biology 5:137–142.

Hoeber, V., and G. Zotz. 2021. Not so stressful after all: Epiphytic individuals of accidental epiphytes experience more favourable abiotic conditions than terrestrial conspecifics. Forest Ecology and Management 479: https://doi.org/10.1016/j.foreco. 2020.118529

Holbrook, N. M., and F. E. Putz. 1996. From epiphyte to tree: Differences in leaf structure nd leaf water relations associated with the transition in growth form in eight species of hemiepiphytes. Plant, Cell & Environment 19:631–642.

Hsu, R. C. C., W. L. Tamis, N. Raes, G. R. de Snoo, J. H. Wolf, G. Oostermeijer, and S. H. Lin. 2012. Simulating climate change impacts on forests and associated vascular epiphytes in a subtropical island of East Asia. Diversity and Distributions 18:334–347.

Hurtado, P., M. Prieto, G. Aragón, F. de Bello, and I. Martínez. 2020. Intraspecific variability drives functional changes in lichen epiphytic communities across Europe. Ecology 101:e03017.

Jian, P. Y., F. S. Hu, C. P. Wang, J. M. Chiang, and T. C. Lin. 2013. Ecological facilitation between two epiphytes through drought mitigation in a subtropical rainforest. PloS One 8:e64599.

Kassambara, A. 2020. ggpubr: 'ggplot2' Based Publication Ready Plots. R package version 0.4.0.

Kassambara, A. 2020. rstatix: Pipe-Friendly Framework for Basic Statistical Tests. R package version 0.6.0.

Kattge, J., G. Bönisch, S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, ... and Cuntz, M. 2020. TRY plant trait database–enhanced coverage and open access. Global Change Biology 26:119–188.

Kluge, J., K. Bach, and M. Kessler. 2008. Elevational distribution and zonation of tropical pteridophyte assemblages in Costa Rica. Basic and Applied Ecology 9:35–43.

Kluge, J. and M. Kessler. 2011. Phylogenetic diversity, trait diversity and niches: species assembly of ferns along a tropical elevational gradient. Journal of Biogeography 38:394–405.

Kluge, J. and M. Kessler. 2008. Morphological characteristics of fern assemblages along an elevational gradient: patterns and causes. Ecotropica 13:27–43.

Kuo, L. Y., C. W. Chen, W. Shinohara, A. Ebihara, H. Kudoh, H. Sato, Y. M. Huang, and W. L. Chiou. 2017. Not only in the temperate zone: independent gametophytes of two vittarioid ferns (Pteridaceae, Polypodiales) in East Asian subtropics. Journal of Plant Research 130:255–262.

Lagomarsino, L. P., A. L. Grusz, and R. C. Moran. 2012. Primary hemiepiphytism and gametophyte morphology in *Elaphoglossum amygdalifolium* (Dryopteridaceae). Brittonia 64:226–235.

Lasso, E. and J.D. Ackerman. 2013. Nutrient limitation restricts growth and reproductive output in a tropical montane cloud forest bromeliad: findings from a long-term forest fertilization experiment. Oecologia 171:156–174.

Laube, S. and G. Zotz. 2003. Which abiotic factors limit vegetative growth in a vascular epiphyte? Functional Ecology 17:598–604.

Lu, H. Z., W. Y. Liu, F. H. Yu, L. Song, X. L. Xu, C. S. Wu, Y. L. Zheng, Y. P. Li, H. D. Gong, K. Chen, S. Li, X. Chen, *et al.* 2015. Higher clonal integration in the facultative epiphytic fern *Selliguea griffithiana* growing in the forest canopy compared with the forest understorey. Annals of Botany 116:113–122.

Mardegan, S. F., G. B. Nardoto, N. Higuchi, F. Reinert, and L. A. Martinelli. 2011. Variation in nitrogen use strategies and photosynthetic pathways among vascular epiphytes in the Brazilian Central Amazon. Brazilian Journal of Botany 34:21–30.

Marks, C. O. and M. J. Lechowicz. 2006. Alternative Designs and the Evolution of Functional Diversity. The American Naturalist 167:55–66.

Nitta, J. H., J. E. Watkins Jr, and C. C. Davis 2020. Life in the canopy: community trait assessments reveal substantial functional diversity among fern epiphytes. New Phytologist 227:1885–1899.

Petter, G., K. Wagner, W. Wanek, E. J. S. Delgado, G. Zotz, J. S. Cabral, and H. Kreft. 2016. Functional leaf traits of vascular epiphytes: Vertical trends within the forest, intra- and interspecific trait variability, and taxonomic signals. Functional Ecology 30:188–198.

Pinson, J. B., S. M. Chambers, J. H. Nitta, L. Y. Kuo, and E. B. Sessa. 2017. The separation of generations: biology and biogeography of long-lived sporophyteless fern gametophytes. International Journal of Plant Sciences 178:1–18.

Pittermann, J., C. B. Brodersen, and J. E. Watkins Jr. 2013. The physiological resilience of fern sporophytes and gametophytes: advances in water relations offer new insights into an old lineage. Frontiers in Plant Science 4:285.

R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rada, F. and R. Jaimez. 1992. Comparative ecophysiology and anatomy of terrestrial and epiphytic *Anthurium bredemeyeri* Schott in a tropical Andean cloud forest. Journal of Experimental Botany 43:723–727.

Reich, A., J. J. Ewel, N. M. Nadkarni, T. Dawson, and R. D. Evans. 2003. Nitrogen isotope ratios shift with plant size in tropical bromeliads. Oecologia 137:587–590.

Rouhan, G., J. Y. Dubuisson, F. Rakotondrainibe, T. J. Motley, J. T. Mickel, J. N. Labat, and R. C. Moran. 2004. Molecular phylogeny of the fern genus Elaphoglossum (Elaphoglossaceae) based on chloroplast non-coding DNA sequences: contributions of species from the Indian Ocean area. Molecular Phylogenetics and Evolution 33:745–763.

Santiago, L. S., K. Silvera, J. L. Andrade, and T. E. Dawson. 2017. Functional strategies of tropical dry forest plants in relation to growth form and isotopic composition. Environmental Research Letters 12:115006.

Schmidt, G. and G. Zotz. 2001. Ecophysiological consequences of differences in plant size: In situ carbon gain and water relations of the epiphytic bromeliad, *Vriesea sanguinolenta*. Plant, Cell & Environment 24:101–111.

Schneider, H., E. Schuettpelz, K. M. Pryer, R. Cranfill, S. Magallón, and R. Lupia. 2004. Ferns diversified in the shadow of angiosperms. Nature 428:553–557.

Schuettpelz, E. and K. M. Pryer. 2009. Evidence for a Cenozoic radiation of ferns in an angiosperm-dominated canopy. Proceedings of the National Academy of Sciences 106:11200–11205.

Stewart, G. R., S. Schmidt, L. L. Handley, M. H. Turnbull, P. D. Erskine, and C. A. Joly. 1995. 15N natural abundance of vascular rainforest epiphytes: Implications for nitrogen source and acquisition. Plant, Cell & Environment 18:85–90.

Suhaimi, N. D. and D. Cicuzza. 2020. The effects of drought and the recovery phase of two tropical epiphytic ferns. Journal of Tropical Plant Physiology 12:33–41.

Sulaiman, S. P. and D. Cicuzza. In Review. Tropical terrestrial and epiphytic ferns have different leaf stoichiometry with ecological implications. 10.21203/rs.3.rs-709718/v1

Testo, W. L. and J. E. Watkins Jr. 2012. Influence of plant size on the ecophysiology of the epiphytic fern *Asplenium auritum* (Aspleniaceae) from Costa Rica. American Journal of Botany 99:1840–1846.

Testo, W. L. and M. Sundue. 2014. Primary hemiepiphytism in *Colysis ampla* (Polypodiaceae) provides new insight into the evolution of growth habit in ferns. International Journal of Plant Sciences 175:526–536.

Turner, E. and W. A. Foster. 2006. Assessing the influence of bird's nest ferns (*Asplenium spp.*) on the local microclimate across a range of habitat disturbances in Sabah, Malaysia. Selbyana 27:195–200.

Watkins Jr, J. E., C. L. Cardelús, R. K. Colwell, and R. C. Moran. 2006. Species richness and distribution of ferns along an elevational gradient in Costa Rica. American Journal of Botany 93:73–83.

Watkins Jr, J. E., M. C. Mack, T. R. Sinclair, and S. S. Mulkey. 2007. Ecological and evolutionary consequences of desiccation tolerance in tropical fern gametophytes. New Phytologist, 176:708–717.

Watkins Jr, J. E., P. W. Rundel, and C. L. Cardelús. 2007. The influence of life form on carbon and nitrogen relationships in tropical rainforest ferns. Oecologia 153:225–232.

Watkins Jr, J. E., C. L. Cardelús., and M. C. Mack. 2008. Ants Mediate Nitrogen Relations of an Epiphytic Fern. New Phytologist 180:5–8.

Watkins Jr, J. E. and R. C. Moran. 2019. Gametophytes of the fern genera *Dracoglossum* and *Lomariopsis* (Lomariopsidaceae) and their phylogenetic significance. International Journal of Plant Sciences 180:1004–1015.

Watts, J. L., R. C. Moran, and J. E. Watkins Jr. 2019. *Hymenasplenium volubile*: documentation of its gametophytes and the first record of a hemiepiphyte in the Aspleniaceae. Annals of Botany 124:829–835.

Wickham, H. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, 2016.

Wickham, H., R. François, L. Henry, and K. Müller 2020. dplyr: A Grammar of Data Manipulation. R package version 1.0.2.

Woods, C. L., C. L. Cardelús, and S. J. DeWalt. 2015. Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. Journal of Ecology 103:421–430.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, *et al.* 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Zhang, S. B., Y. Dai, G. Y. Hao, J. W. Li, X. W. Fu, and J. L. Zhang. 2015. Differentiation of water-related traits in terrestrial and epiphytic *Cymbidium* species. Frontiers in Plant Science 6:260.

Zhang, S., Y. Yang, J. Li, J. Qin, W. Zhang, W. Huang, and H. Hu. 2018. Physiological diversity of orchids. Plant Diversity, 40:196–208.

Zotz, G. and P. Hietz. 2001. The physiological ecology of vascular epiphytes: Current knowledge, open questions. Journal of Experimental Botany, 52:2067–2078.

Zotz, G., P. Hietz, and G. Schmidt. 2001. Small plants, large plants: The importance of plant size for the physiological ecology of vascular epiphytes. Journal of Experimental Botany, *52*:2051–2056.

Zotz, G. and U. Winkler. 2013. Aerial roots of epiphytic orchids: the velamen radicum and its role in water and nutrient uptake. Oecologia 171:733–741.

Zotz, G. 2016. *Plants on plants-the biology of vascular epiphytes.* Switzerland: Springer International Publishing.

American Fern Journal 111(4):327–331 (2021)
Published on 5 November 2021

Shorter Note

Discovery of Mixed Sporangia in the Amazonian Quillwort *Isoëtes cangae*.— South America is a center of taxonomic diversity for *Isoëtes*, with an estimated number of 64 species (Troia *et al.*, Phytotaxa 277:101–145. 2016). *Isoëtes cangae* J.B.S. Pereira, Salino & Stützel is an endemic species in the Amazon region with distribution restricted to a single lake (Pereira *et al.*, Phytotaxa 272:141–148. 2016), and is considered critically endangered (Lansdown, The IUCN Red List of Threatened Species 2019: e.T136249847A136250011. 2019). It is heterosporous, as are all *Isoëtes* species, with demonstrated sexual reproduction (Caldeira *et al.*, Aquatic Botany 152:51–58. 2019).

The megaspores and microspores of *Isoëtes* are usually produced in distinct structures, megasporangia and microsporangia, respectively, and their proportion in the rosette varies through the year (Voge, Limnologica 36:228–233. 2006; Campos *et al.*, Limnologica 89:125889. 2021). Atypically, mixed sporangia containing both megaspores and microspores were found in some individuals of *Isoëtes cangae* growing in the natural habitat. This character has been reported in some species of *Isoëtes*, such as *I. taiwanensis* (DeVol, Taiwania 17:1–7. 1972) and *I. yunguiensis* (Qing-Feng and Xing, Novon 12:587–591. 2002). Goswami and Arya (British Fern Gazette 10:39—40. 1968) also found sporangia containing two types of spores ("intrasporangial heterospory") with low occurrence in *I. pantii*, which have been shown to be viable (Goswami and Bhu, Bionature 20:9–18. 1998). The third type of spore resembling an ancestral lineage was observed in *I. pantii* sporangia, and this kind of sporangium with three distinct spore morphologies was named a heterosporangium (Goswami, Acta Botanica Hungarica 56:77–92. 2014).

The factors that induce formation of mixed sporangia and their implications for species reproduction are still largely unknown. Is it a condition genetically determined? Do the spores in the mixed sporangia differ from those of a unisexual sporangium? Are they fertile? To address these important questions, we have investigated the morphology and viability of spores found in the mixed sporangia of *I. cangae*.

Specimens of *I. cangae* were collected in lake Amendoim, in the south range of the Serra dos Carajás, Pará, Brazil. Of the twelve individuals sampled in June 2019, only one showed seven mixed sporangia (24% of the sporangia from this specimen). In February 2020, two of fifteen individuals sampled in the lake, presented 2-3 mixed sporangia (3% of the sporangia from these specimens). Mixed sporangia from both collections were dissected to count the number of megaspores per sporangium. Each mixed sporangium from the June 2019 collection contained an average of 75 megaspores, and 110 from the February 2020 collection. The spore number per megasporangium in *I. cangae* is a variable character (Cavalheiro-Filho *et al.*, American Fern Journal 111:174–185. 2021) and was reported to range between 78-166 (Caldeira *et al.*, 2019).

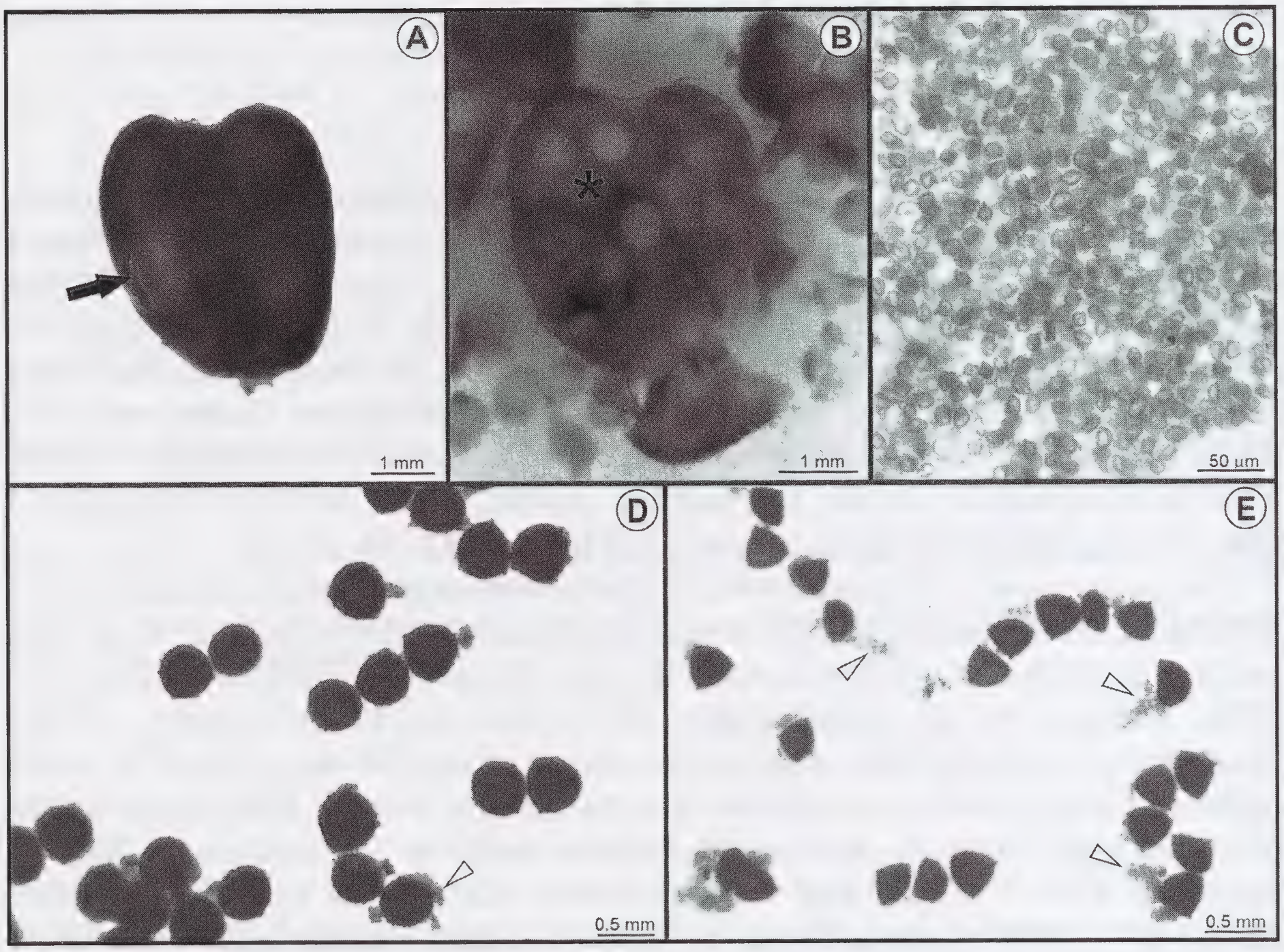

Fig. 1. Mixed sporangia of *Isoëtes cangae* collected in June 2019 (A-C) and February 2020 (D-E). A. Abnormal sporangia with undulations on the surface (arrow). B. Opened sporangium showing megaspores and microspores (asterisk). C. Microspores isolated from a mixed sporangium. D-E. Oblate-spheroidal megaspores (D) and smaller tetrahedral megaspores (E), from a single mixed sporangium, intermixed with microspores (white triangles).

The mixed sporangia were observed and photographed using a stereomicroscope with a digital camera. They presented an abnormal morphology with undulations on the surface, due to the presence of megaspores, and a dense content related to the numerous microspores (Fig. 1 A-C). Among the mixed sporangia collected in February 2020, only one was considered mature and was used for micromorphometric measurements of megaspores. The measurements were taken using Image-Pro Plus 4.5 software (Media Cybernetics, Silver Spring, USA). Two types of megaspores were observed in this sporangium: oblate-spheroidal megaspores (n = 108; diameter = 479.7 µm), and tetrahedral smaller megaspores (n = 42; diameter = 336.0 µm) (Fig.1 D-E).

The mixed sporangia collected in June 2019 were used for self-fertilization tests. The male (100 µl of concentrated spore suspension) and female spores (n=10) were put together in 15 ml falcon tubes with non-sterile distilled water. After two months of monitoring, the emergence of 28% sporophytes was recorded. To evaluate the development of sporophytes derived from spores of mixed sporangia, the sporophytes were transferred to 2.0 L pots containing pond sediment and sand. After fifteen months, the sporophytes grew to ±12

cm in length and contained 34 leaves. None of these F2 generation individuals presented mixed sporangia and all of them were able to reproduce (Fig. 2). On average, these plants generated 19 sporelings spontaneously, comprising the third generation. These results confirm that spores from mixed sporangia are viable and produce fertile sporophytes. The simultaneous presence of homosporangia and mixed sporangia in the same individual suggests that differentiation of sporangia is probably influenced by environmental conditions. In homosporous ferns, several environmental factors play a role in the gender expression of gametophytes (DeSoto, Quintanilla, and Méndez, Journal of Ecology 96:1319–1327. 2008).

An additional experiment was carried out to evaluate the viability of both types of megaspores from the mature mixed sporangia collected in February 2020. They were cultivated separately (n=15) in the presence of microspores from normal microsporangia. The tests were done in triplicate using 15 ml tubes filled with non-sterile distilled water. After 30 days, 60% of the normal-shaped megaspores formed sporophytes while none of the smaller megaspores germinated. The percentage of sporophytes formed from oblate-spheroidal megaspores (normal shaped) was similar to that reported for megaspores from megasporangia of this same species, which was 63% (Caldeira *et al.*, 2019). We demonstrated that the smaller spores of *I. cangae* are sterile, as reported by Goswami (2014) for *I. pantii*. A large number of abortive spores may represent a selective process, as a means to accommodate the size and number of spores according to the limited nutrition and nurturing space (Goswami, 2014). The low percentage of sporophyte formation in the samples of June 2019 can be explained, at least partially, by the presence of abortive spores, which were not previously investigated.

Many species of *Isoëtes* are often characterized by producing dimorphic spores within the same sporangium, which are different in shape and size (Srivastava *et al.*, American Fern Journal 82:162–170, 1992). The diameter of megaspores from megasporangia of *I. cangae* is about 500 μm (Pereira *et al.*, 2016; Cavalheiro-Filho *et al.*, 2021), which is 1.5 times greater than those reported in this study for tetrahedral megaspores. The oblate-spheroidal megaspores were normal sized. According to DeVol (1972) and Qing-Feng & Xing (2002), megaspores in mixed sporangia can be slightly smaller than those found in the normal sporangia. Additionally, microspores from mixed sporangia of *I. cangae* also seem to vary in size and shape (Fig 1C). The presence of dimorphic megaspores and microspores within the same sporangium may be related to different types of spore mother cells, which was considered an ancestral condition in *I. pantii* (Goswami, 2014).

The presence of mixed sporangia was reported for the first time in an American *Isoëtes*. Its frequency is low within the population, and its occurrence varies among individuals. Further investigation of the factors involved in the differentiation of mixed sporangia in *I. cangae* are needed to understand the reproductive mechanisms of this endemic and critically endangered Amazonian quillwort.

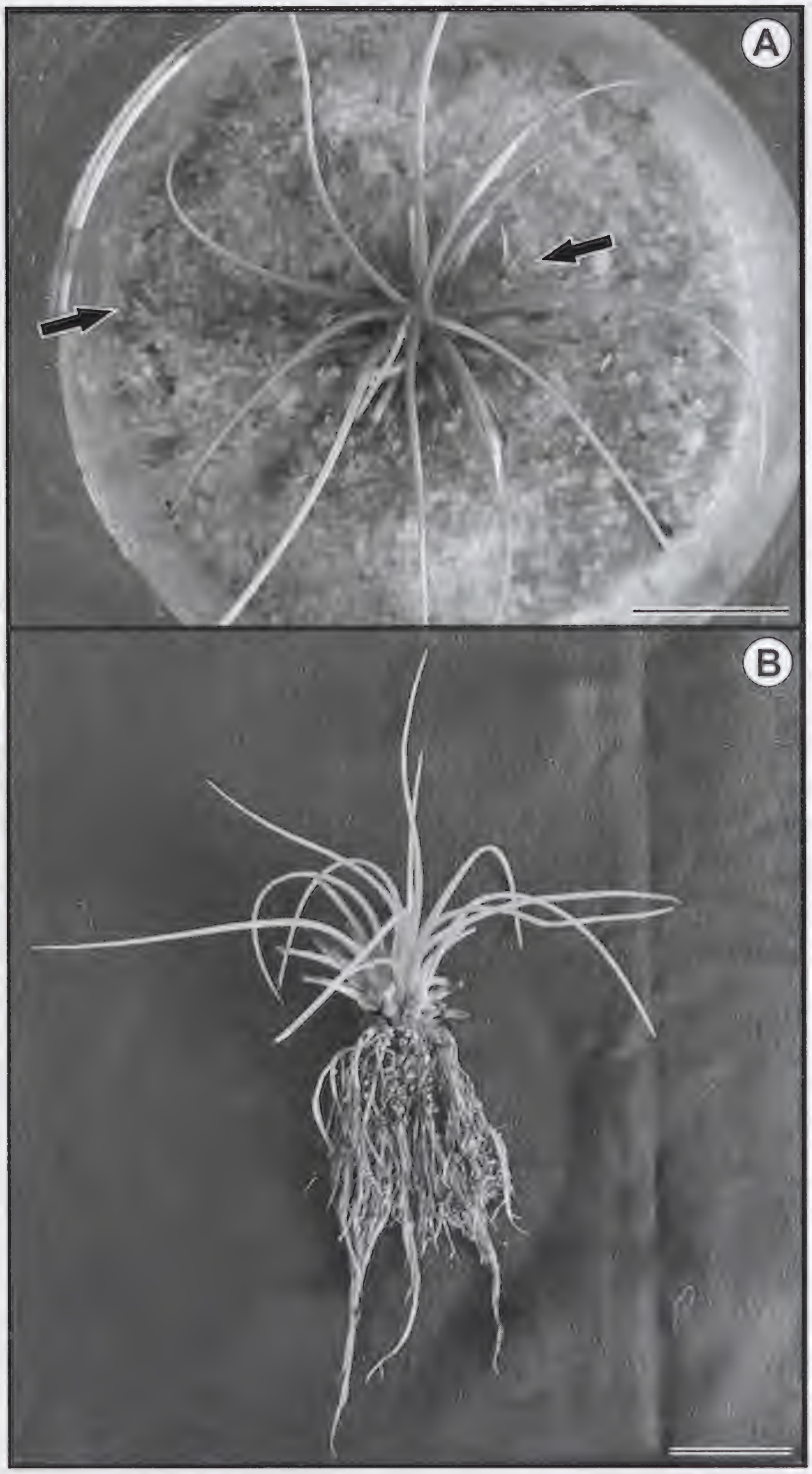

Fig. 2. Sporophytes generated from the crossing of spores contained in mixed sporangia of *Isoëtes cangae*. A. Adult plant and new sporophytes (arrow) representing the third generation. B. Typical morphology of an adult sporophyte (second generation). Bar = 3 cm.

ACKNOWLEDGMENTS

We thank Emiliano N. Calderon, Mariana C.H. Marques, Luis A.S. Prado, and Anderson R. Gripp for supporting the field work. We also thank the Chico Mendes Institute for Biodiversity Conservation (ICMBio/MMA) for supporting the studies in the Carajás National Forest, under license number 64403. NAIARA VIANA CAMPOS[1*] (Email: naiaravcampos@gmail.com); SERGIO LUÍS CAVALHEIRO-FILHO[1]; LAÍS B. JORDÃO[1]; FERNANDO M.G. SANTOS[2]; ALEXANDRE CASTILHO[2]; RODRIGO L. MARTINS[1]; FRANCISCO A. ESTEVES[1]; LÍSIA M.S. GESTINARI[1]. [1]Instituto de Biodiversidade e Sustentabilidade NUPEM, Universidade Federal do Rio de Janeiro, Caixa Postal 119331, 27901-000, Macaé, Rio de Janeiro, Brazil. [2]Vale S.A., Gerência de Estudos Ambientais, 34006-200, Nova Lima, Minas Gerais, Brazil.

INFORMATION FOR AUTHORS

Authors are encouraged to submit manuscripts pertinent to the study of ferns and lycophytes for publication in the *American Fern Journal*. Manuscripts should be submitted to http://www.editorialmanager.com/afj/. Acceptance of papers for publication depends on merit as judged by two or more referees. Authors are encouraged to contribute toward publishing costs; however, the payment or non-payment of page charges will affect neither the acceptability of manuscripts nor the date of publication. Mandatory fees will be charged for color figures in print and/or in electronic versions of published papers.

Information for authors, including detailed requirements for formatting manuscripts can be found online at: https://www.amerfernsoc.org/american-fern-journal/.

FOR INFORMATION REGARDING AVAILABLE PUBLICATIONS, VISIT THE AMERICAN FERN SOCIETY'S WEBSITE: http://amerfernsoc.org/

The "American Fern Journal" (ISSN 0002-8444) is an illustrated quarterly devoted to the general study of ferns. It is owned by the American Fern Society, and published at The American Fern Society, c/o 926 W. Campus Drive, MC 0406, Blacksburg, VA 24061-1040. Periodicals postage paid at Blacksburg, VA, and additional entry.

Claims for missing issues, made 6 months (domestic) to 12 months (foreign) after the date of issue, and orders for back issues should be addressed to Dr. George Yatskievych, Plant Resources Center, University of Texas at Austin, Main Bldg, Rm 127, 110 Inner Campus Dr, Stop F0404, Austin, TX 78712-1711; e-mail: george.yatskievych@austin.utexas.edu

Changes of address, dues, and applications for membership should be sent to the Membership Secretary.

General inquiries concerning ferns should be addressed to the Secretary.

Back volumes are available for most years as printed issues. Please contact the Back Issues Curator for prices and availability. Digital versions of back issues three years or older are available free online through the Biodiversity Heritage Library: http://www.biodiversitylibrary.org/bibliography/43943#/summary

Subscriptions Rates per Volume for electronic access:

Student/Non-academic membership	$20
Academic membership	$40
Lifetime membership	$600
Libraries, Herbaria, & Commercial Organizations	$60

Print access to the journal is available for an additional $20/year

POSTMASTER: Send address changes to American Fern Journal, c/o Sally Chambers, Botany Department, Marie Selby Botanical Gardens, 1534 Mound St., Sarasota FL 34236.

SMITHSONIAN LIBRARIES
3 9088 02039 5349

AMERICAN
FERN JOURNAL

VOLUME 111 NUMBER 4 October-December 2021

Looking Back on 130 Years of Fern and Lycophyte Research in Glacier National Park, Montana: A Modern Taxonomic Account
Keegan Heron, Michael D. Windham, Donald R. Farrar, and Kathleen M. Pryer 223

The Scaly Tree Ferns Allied to *Cyathea multiflora* (Cyatheaceae) in Colombia and Neighboring Countries
Marcus Lehnert, Adrian Tejedor, Wilson D. Rodríguez Duque, and Luis Fernando Giraldo Gallego 251

Crossing the Divide: An Exploration of Functional Traits in Ferns that Grow Across Terrestrial, Epipetric, and Epiphytic Habitats
Jacob Lewis Watts and James E. Watkins, Jr. 308

SHORTER NOTE

Discovery of Mixed Sporangia in the Amazonian Quillwort *Isoëtes cangae*
Naiara Viana Campos, Sergio Luís Cavalheiro-Filho, Laís B. Jordão, Fernando M.G. Santos, Alexandre Castilho, Rodrigo L. Martins, Francisco A. Esteves,and Lísia M.S. Gestinari 327

COVER CAPTION: *Cyathea hildegardis*. Colombia. Photo credit: Luis Fernando Giraldo Gallego